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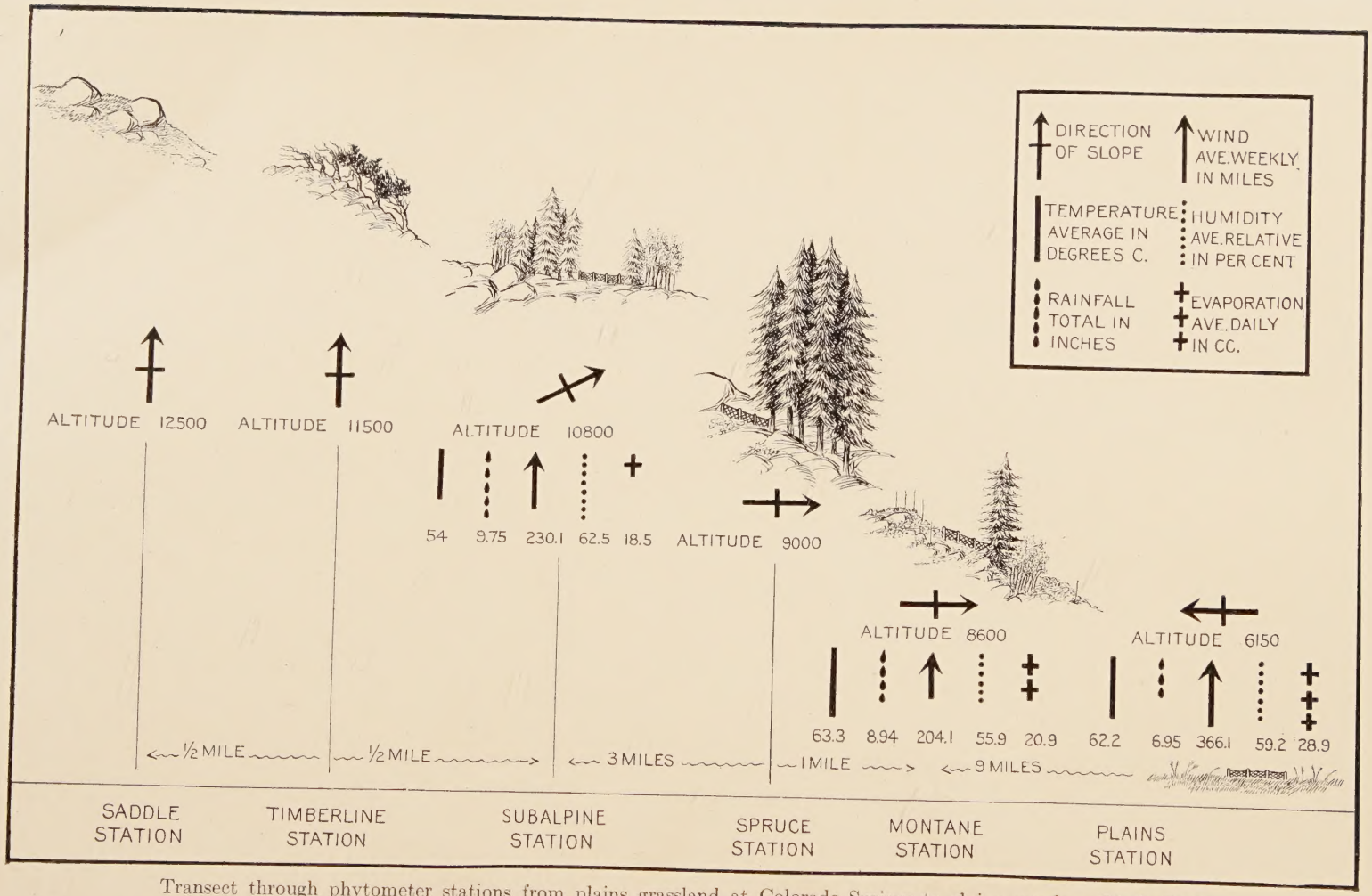

Transect through phytometer stations from plains grassland at Colorado Springs to alpine meadow, Pike's Peak.

THE PHYTOMETER METHOD IN ECOLOGY

THE PLANT AND COMMUNITY AS INSTRUMENTS

q66

BY

FREDERIC E. CLEMENTS AND GLENN W. GOLDSMITH

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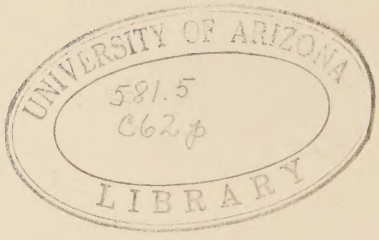

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THE PHYTOMETER METHOD IN ECOLOGY.

SCOPE AND ESSENTIALS.

NATURE OF QUANTITATIVE ECOLOGY.

The first attempt to organize ecological research upon a quantitative basis was made in "Research Methods in Ecology" nearly 20 years ago. While this has met with much success, it is not yet generally recognized that the term ecology connotes a study of the relation between organism and habitat, which demands the use of exact methods. For this reason it appears fortunate that the floristic study of vegetation, so much in vogue on the continent of Europe, is rapidly coming to be known as plant sociology. To the ecologist, however, the cause-and-effect relation between plant and habitat is more than ever "the central and vital part of botany," in the investigation of which quantitative methods alone can yield results of fundamental and permanent value. The emphasis given to this as a guiding principle in "Research Methods" may be recalled with profit at the present time.

"In seeking to lay the foundation for a broad and thorough system of ecological research, it is necessary to scan the whole field and to discriminate carefully between what is fundamental and what is merely collateral. The chief task is to discover, if possible, such a guiding principle as will furnish a basis for a permanent and logical superstructure. In ecology, the one relation that is precedent to all others is the one that exists between the habitat and the plant. This relation has long been known, but its full value is yet to be appreciated. It is precisely the relation that exists between cause and effect, and its fundamental importance lies in the fact that all questions concerning the plant lead back to it ultimately. Other relations are important, but no other is paramount, or able to serve as the basis of ecology. Ecology sums up this relation of cause and effect in a single word, and it may be that this advantage will finally lead to its general acceptance as the proper name for this great field.

"Any serious endeavor to find in the habitat those causes which are producing modification in the plant and in vegetation can not stop with the factors merely. The next step is to determine the quantity of each. It is not sufficient to hazard a guess at this, or to make a rough estimate of it. Habitats differ in all degrees and it is impossible to institute comparisons between them without an exact measure of each factor. It is of little value to know the general effect of a factor, unless it is known to what degree this effect is exerted. For this purpose it becomes necessary to appeal to instruments, in order to determine the exact amount of each factor that is present in a particular habitat, and hence to determine the ratio between the stimulus and the amount of structural adjustment that results. The employment of instruments of precision is clearly indispensable for the task which we have set for ecology, and every student that intends to strike at the roots of the subject and to make lasting contributions to it, must familiarize himself with instrumental methods."

ADVANTAGES OF INSTRUMENTS.

The improvement of meteorological instruments made it possible to begin the measurement of habitats with a considerable equipment and to devise new or modified types. The chief lack was with respect to instruments for determining water-content and light, the two most important factors to the plant. This was met by the development of a series of photometers, as well as various kinds of geotomes and soil-borers. However, these were less available than the standardized meteorological instruments, which came to constitute the usual equipment for factor studies, with the addition of the porous-cup atmometer. These had the further advantage of being more or less familiar and their readings were expressed in terms readily understandable, and they also made it possible to compare the observations taken in a particular habitat with the records of the same factors accumulated by weather bureaus, and thus to broaden the scope of the investigation. The development of recording instruments for temperature, humidity, light, wind, etc., greatly increased the effective range of the worker and conserved both his time and energy. Finally, the complete battery of physical instruments came to have a new value in interpreting the results obtained from phytometers and often by converting them into more intelligible terms.

DISADVANTAGES OF INSTRUMENTS.

A fundamental and inevitable drawback to all instruments is the failure to express factor differences in terms of the plant. The objection has often been made that it is possible to measure all the major factors of a habitat without an adequate return in determining the behavior of the plants themselves. While this is partly due to the lack of quantitative studies of functions under field conditions, it arises chiefly from our present inability to express physiological activity in terms of physical factors, a condition that the phytometer method is designed to remedy. A further disadvantage lies in the fact that accuracy is greatest with the instruments that measure the less important indirect factors, such as temperature, wind, and pressure, and least with those for determining the direct factors, humidity, water-content, and light. Moreover, the recording instruments are in general less accurate than the simple ones, and their increased cost in recent years has practically put them out of the reach of the individual investigator. Existing recorders need to be simplified in some cases and new instruments should be devised in others, with especial consideration of the fact that the cost of a complete battery of ecological instruments has greatly retarded adoption of quantitative methods in ecology; even more critical is the failure of most instruments to integrate the factors concerned, since measurements of function are regularly obtained as sums. It is this consideration, coupled with the plant's judgment as to efficient factors, that makes the phytometer indispensable to quantitative ecology.

PLANT'S RELATION TO FACTORS.

The distinction between direct and indirect factors is prerequisite to a proper understanding of the relations of plant and habitat (Clements, 1907). A direct factor is one that produces an immediate response in function, such

as water, light, or oxygen, while an indirect one affects the plant only through some direct factor. In short, the measurement of direct factors furnishes the clue to the behavior of plant or community, while that of indirect factors helps to explain the amounts of direct ones present. In the majority of habitats the determination of water-content, humidity, and light suffices for a fairly complete understanding of plant behavior, and the measurement of indirect factors is important chiefly in the comparative study of habitats. Moreover, the decision as to the amount or intensity of any factor necessary to produce a change in function or structure can be rendered only by the plant. The sensibility of instruments is often greater than that of the plant, and this sometimes gives a fictitious significance to the results. The efficiency of a direct factor can be determined only by the response made by the plant or group, and hence it will necessarily vary with the plants concerned. On the other hand, the effectiveness of indirect factors is measured by the consequent modification of direct ones, and not by an immediate action upon the plant. Thus, while the factors of a habitat may be readily ascertained by means of instruments, their significance in the development or structure of the plant or community must be determined by the latter. In this lies the essence of the phytometer method. Effects must be determined by the plant, and the factor intensities that produce them must be measured by instruments.

POSSIBILITY OF USING PLANTS AS MEASURES.

In a general way, plants serve as measures of conditions wherever they grow. This is the principle that underlies the indicator value of native plants.[a] It operates with equal force in the case of cultivated plants and crops of all sorts, though with these it must be recognized that the habitat has been artificially modified to some degree. Whenever a species is planted under new conditions of soil or climate, it serves as a kind of practical phytometer by comparison with its usual growth. To give this definite value it is necessary to measure its response along with the conditions that control it. This has led to the use of standard plants, selected from species that grow vigorously under control and offer few difficulties in handling and measuring. At present certain cultivated plants constitute the best biological instruments, but it is possible that some native species will prove less variable. In addition to this use, it is to be expected that cultivated plants will be most successful as phytometers for cropping conditions and native ones for the natural habitats with which forestry and grazing are concerned.

In the first attempts to develop a method, leafy shoots were employed in potometers with considerable success. With the growing recognition of the sharp limitations of potometers, this practice has been discontinued, though under proper checks and for short periods it still has a certain value. The paramount consideration in using phytometers is that each battery should exhibit the actual effect of the habitat and not mask this by the variability of the individuals. This difficulty has been met in various ways,

[a] Carnegie Inst. Wash. Pub. No. 290, 1920.

as indicated later. It is eliminated to a large degree when the number of plants is large, as in a crop plot or a transplanted quadrat.

PRELIMINARY USES OF PLANTS.

While the intentional use of plants as instruments for measuring factors dates from 1906, the essence of the method is to be found not only in all experimental planting, but also in the comparative study of growth and function under different conditions by means of pot cultures. This is especially true of the chresard-echard investigations from the early studies of Sachs (1859, 1865), Heinrich (1874), and Mayer (1875) to those of Gain (1895), Clements (1900, 1904), Hedgcock (1902), Briggs and Shantz (1912), and Crump (1913). The method was actually initiated when plants were put in different conditions in the field, though in most of this work attention was directed to the plants as affected by the factors rather than as measures of them. The next step in advance was to employ plants as instruments in measuring the effects of different habitats, and the present stage is represented by the series of investigations designed primarily to develop the phytometer method into an indispensable tool for the quantitative ecologist.

The earliest example of the first step was afforded by the classic experiments of Bonnier (1890), in which he made reciprocal plantings of alpine and lowland plants. This was the first important application of the transplant method, which has been developed into one of the most significant uses of the phytometer, but it led to no further advance, probably because Bonnier's interest in factors was secondary and did not result in the measurement of them. Clements (1904 : 26; 1905 : 33, 115) employed plants to determine the chresard of different soils in the field, under measured conditions of the various direct factors. Hesselmann (1904 : 413, 379) made use of potometers and potted plants of several native species to determine the transpiration in sun and shade, in addition to the use of leaves for ascertaining the relative photosynthesis and respiration. Sun and shade forms of various polydemic species were isolated in soil blocks, and the water-loss determined by weighing on the spot. He also studied the structural response of the leaves to sun and shade, and this phase of the problem was carried much further by the extensive investigations of E. Clements (1905) on the behavior of ecads under measured conditions in the Rocky Mountains. The first use of plants for the express purpose of measuring physical factors in different habitats was that of Clements (1907 : 287; 1907[2] : 65), who employed potometers of native species for determining the efficiency of the factors involved in altitude, and potted sunflowers as standard plants to supplement the instrumental readings in different seral habitats. Sampson and Allen (1909 : 45) used potometer batteries of native species to determine the comparative transpiration of four habitats provided with instruments, as well as to measure the reciprocal water-loss of sun and shade forms of the same species, and the effect of altitude on transpiration.

Planting in different situations to determine the comparative behavior of seedlings has been practiced chiefly by foresters. Pearson (1914 : 253) employed seedlings of Douglas fir to ascertain the effect of aspen cover on

establishment and growth, placing 100 plants in each of two plots in the open and two under aspen. The greater success under aspen was ascribed to reduced transpiration, as indicated by the fact that evaporation was 50 to 100 per cent less. In a study of the subclimax nature of aspen forest, Baker (1916 : 294) made use of yellow pine, Douglas fir, Engelmann spruce, and Norway spruce, planting them in several light intensities from 0.09 to 1. With the exception of the intolerant yellow pine, which did best at 0.3, ecesis increased with decreased light and was greatest at the lowest intensity. Hole and Singh (1916 : 241) installed experimental quadrats in sal forests to determine the effect of aeration and light upon the germination and growth of sal seeds. The open plots gave 48 per cent of germination and 21 per cent of healthy plants in contrast to 26 and 2 per cent respectively for the shade ones. Similar quadrats were employed to disclose the consequences of removing the forest cover, the shade and cleared plots giving respectively 71 and 91 per cent of germination and 34 and 51 per cent of healthy plants, height growth in the open being 2.5 times as great. Iljin (1916 : 65) made use of potometers to determine the transpiration and photosynthesis of various mesophytes and xerophytes in different habitats, and McLean (1919) employed leaf potometers for water-loss in rain-forests.

Beginning with 1916, the use of standard plants as instruments underwent further development (Clements, 1916 : 439; Livingston and McLean, 1916 : 362). The first extensive investigation was that of McLean (1917 : 129), which was "an attempt to test certain methods for determining some of the quantitative relations between climatic conditions and the growth of plants. The plant is thus regarded as a sort of integrating and recording instrument, the reading of which is zero at the beginning of each observation period." The standard plant employed was soy-bean grown from seed for each observation period. The plants were all grown in the same soil in pots furnished with auto-irrigators, and in consequence temperature, evaporation, and sunshine were the conditions studied. The two stations considered were Oakland in the mountains of western Maryland and Easton on the eastern shore of Chesapeake Bay. The growth measurements taken each month were stem-height, average number of leaves per plant, average length and width of mature leaves, and average of the products obtained by multiplying length by width for each leaf, supplemented by average leaf-area and average dry weight of tops per plant. It was found that temperature was the limiting condition for growth during the first two weeks, while the moisture relation was largely controlling for the second two weeks, especially when the temperature was high.

Weaver and Thiel (1917 : 47) employed woody seedlings as well as potometers to measure the transpiration relations of prairie, scrub, and forest at Lincoln and Minneapolis. A considerable number of native trees and shrubs were utilized, comprising *Quercus macrocarpa, Acer saccharinum, A. negundo, Ulmus americana, Fraxinus lanceolata, Prunus serotina,* and *Rosa arkansana.* Both sun and shade forms were used in the case of the latter. Marked differences were disclosed between the various communities; for example, the transpiration in oak forest was less than a half

of that in hazel scrub, and the water-loss in the latter less than a third of that in the prairie. The most significant fact was the wide discrepancy between evaporation as determined by the porus-cup atmometer and the transpiration from phytometers, amounting in some cases to 100 per cent. The series of studies designed to develop the phytometer as a basic method in quantitative ecology was begun in 1918, and preliminary accounts of its progress have been made from year to year, as follows: Clements and Weaver, 1918; Clements, Weaver, and Goldsmith, 1919, 1920, 1921, 1922; Clements and Goldsmith, 1923; Clements, 1920 : 42, 45, 70.

Sampson (1918) has made the most comprehensive investigation of habitat factors on the basis of standard plants, employing *Pisum sativum, Triticum durum,* and *Bromus marginatus* for this purpose. The climatic factors concerned were those of the Petran chaparral above 6,500 feet, the montane forest above 7,500 feet, and the subalpine forest from 9,000 to 11,000 feet, the stations being located at 7,100, 8,700, and 10,000 feet. Leaves and stems were measured first at 10-day and then at monthly intervals, and the dry weight and ash-content were determined at the end of the growing season. The water requirement was found to be greatest in the chaparral, less in the subalpine forest, and least in the montane climax, while the length of stem was also greatest in the chaparral and least in the montane type, the production of dry matter being just reversed. An especially significant result lay in the indications as to cropping possibilities furnished by the Kubanka wheat and Canadian field pea.

The development of transplant phytometers in contrast to the use of standard plants was begun in 1919, and the essentials of the method are now practically complete (Clements and Weaver, 1919–1923; cf. Experimental Vegetation, 1924). The climatic series comprises stations ranging from a rainfall of 35 inches in eastern Nebraska to one of 15 inches at Colorado Springs, while the edaphic runs from swamp at the hydrophytic extreme through low and high prairie to gravel-knoll and salt-flat at the xerophytic end. In addition, the two transects for experimental evolution, the Petran at Pike's Peak and the Sierran from the Pacific Coast through the Sierra Nevada to the desert, also yield phytometric data of great climatic value. To the same general category belong clip and production quadrats, which serve to compare the efficiency of different regions, seasons, or years (Weaver, 1921 : 400; 1924; Taylor and Loftfield, 1922; 1923). Finally, a combination of phytometer methods has been employed in the analysis of the factor-complex on opposite slopes at the Alpine Laboratory (Clements and Lutjeharms, 1921, 1922; Lutjeharms, 1924).

Hildebrandt (1921 : 341) has presented a complete account of the investigation into climatic conditions and plant growth made by McLean, who reported the results for two stations, as already indicated (p. 7). Nine stations were concerned, and the standard plant employed was the soy-bean. The factors determined were air temperature, evaporating power of the air, and sunlight intensity and duration, while the plant measurements taken were stem-height, leaf-area, leaf-product, and dry weight. Johnston (1921 : 41) has made a similar study of the atmospheric conditions of a greenhouse with respect to an unshaded portion and a cheese-

cloth shade-tent. Plants of buckwheat were used as standards, being grown for 4-week periods through 13 months. The factors measured were temperature, evaporation, and radiation, and the plant responses determined at regular intervals were stem-height, leaf-area, transpiration, and dry weight.

KINDS OF PHYTOMETERS.

As is evident, the term *phytometer* (φυτόν, plant; μέτρον, measure) denotes a plant measure, and is employed for either a single plant or a plant group. In general, the distinction between the two types is convenient if not natural, but it must be recognized that individual phytometers are regularly arranged in batteries of several to many, while group phytometers may often be analyzed into individuals. Moreover, it is sometimes desirable to grow more than one plant in a single container. The difference is most clearly shown by standard plants in sealed containers on the one hand and by clip, crop, or transplant quadrats on the other. Phytometers may further be distinguished as natural when native plants, or indicators, are utilized in position, and as artificial when they are specially grown or transplanted as measures. Control phytometers are those in containers, which permit the control of one or more factors, especially in the soil, and allow the plants to be moved about for checking or transferring. Free phytometers are planted in the soil and are subject to the factor-complex of the habitat, though a certain amount of control may be exerted by means of watering, shading, covering, etc. Climatic phytometers are those in which the effect of soil factors is eliminated by rendering these uniform in sealed containers, while edaphic ones are characterized by different soil habitats within the same local climate.

CONTROL PHYTOMETERS.

These consist of cultivated or native species in sealed or open containers. With sealed containers the effect of rainfall is eliminated and the direct factors concerned are humidity, temperature, and light. Open containers with the same soil give the total climatic effect, and when checked against sealed ones furnish evidence of the influence of varying rainfall through the direct factor, water-content. If open containers with soils from the different habitats are added to the battery, it becomes possible to distinguish the effects of air and soil factors. Still further differentiation of the control is possible, but at present it is desirable only with crop plants.

It seems preferable to restrict the term standard plant or standard phytometer to cultivated species, since these are readily obtained and grown in nearly all regions. They are likewise more dependable than native species, as most of the latter require a special study before satisfactory germination and growth can be secured. For this reason cultivated plants are especially desirable when growth is one of the responses to be measured. It is obvious that they should be employed when phytometers are to furnish information with reference to cropping possibilities and methods. For this purpose the preferred species is the one actually to be grown, or one as nearly like it as possible in its demands. In accordance with the

same principle, native plants should be used in the study of forest and range, a widespread species such as *Pinus ponderosa* or *Stipa comata* being preferable for climatic comparisons. In phytometer batteries the widest range of results is obtained by the use of both cultivated and native plants.

TRANSPLANT PHYTOMETERS.

Free phytometers may be grown in place, or transferred from another habitat or the greenhouse in which they have been started. When the whole process of ecesis is to be taken into account, seeding is imperative, but the greater certainty obtained by the use of plants causes transplanting to be the more profitable method, particularly when physical factors alone are to be measured. If the total effect of the habitat is to be analyzed in terms of factors, competition, and animals, both seeds and transplants must be employed. When habitats, local or formational, are to be compared, plants are subjected to the total impact of the factor-complex, but some degree of control is necessary to determine the influence of particular factors or to enable seedlings or transplants to pass the initial stage successfully. This is secured by watering, aerating, shading, thinning, covering against frost or winter-killing, etc. A further degree of control, and hence of analysis, is obtained by seeding or planting in soil-pockets or in quadrats made uniform as to soil, or in the different natural soils of the same climate. The methods and technique of transplant phytometers have been worked out in detail in connection with the three climatic and one edaphic experimental transects already mentioned, but their discussion is to be found in the volume on experimental vegetation (Clements and Weaver, 1924).

INDICATOR PHYTOMETERS.

Every indicator plant is a potential phytometer of greater or less value, requiring only measurements and factor readings to convert it into an actual one. In nature these measure the total habitat, but they may be treated very like transplant phytometers to yield various degrees of analysis. They may be protected to give total growth unaffected by grazing, or watered or covered to equalize certain factors. They may even be replaced in uniform soil to disclose the climatic effect, when they approximate transplant phytometers. They permit measurements of growth, photosynthesis, or respiration as readily as do control phytometers, but they must be cut out in soil-boxes to furnish transpiration weighings. Indicator plants possess the unique value of being already established, as well as adapted to conditions, and for this reason afford a helpful check upon transplant and control phytometers.

COMMUNITY PHYTOMETERS.

These consist of a group of individuals of one or more species in the reciprocal relation to each other that obtains in a natural community or in a cultivated field. They may vary much in size, but that of the meter quadrat possesses distinct advantages. Like individual phytometers, they may be either natural, planted, or transplanted, or even employed in containers, though the latter form has as yet been little developed. The clip-

quadrat constitutes the best example of the natural phytometer, as the growth habit of grasses makes this much more useful than a cut-quadrat in scrub or forest. In the natural condition it furnishes a measure of the combined influence of factors, competition, and animals, but it may be so controlled by protection as to eliminate the latter, or to equalize certain factors. It is much more difficult to remove competition, and the rôle of the latter can best be determined by means of individual phytometers, in which competition is lacking. The transplanting of communities to serve as phytometers is practicable only in the case of cryptogams, especially lichens and mosses, small or seedling families and colonies, or portions of herbaceous communities, particularly of the sod-forming type. In moving meter quadrats of alpine meadow from the summit of Pike's Peak to the Alpine Laboratory, it was necessary to divide them into smaller squares, and this would be even more imperative in the case of taller or deeper-rooted vegetation. While scrub and tree groups can be transplanted in the seedling stage, the labor is so great that it is much more feasible to use seeding or planting quadrats for the results desired. Such quadrat phytometers are essentially alike in nature and treatment, whether located in forest, range, or cultivated field. They are usually more successful in the latter, owing to the use of cultivated plants, protection against mishaps, and the opportunity for further control.

RESPONSES MEASURED.

Functions permit of readier and more exact measurement than changes of structure, while growth offers peculiar advantages as a process intermediate between the two. Naturally, such functions as transpiration and photosynthesis, which are controlled by highly variable factors—water, light, and temperature—are much more significant than respiration. For evaluating the relative efficiency of holard and humidity, transpiration is of paramount importance, especially when stomatal behavior is taken into consideration. In the case of light, photosynthesis is similarly all-important. Rate of growth and total growth, expressed in various forms, reflect both transpiration and photosynthesis, but the great value lies in the fact that growth sums up the effect of practically all factors. It may be measured at regular intervals in terms of stem and leaf, or expressed at the end as dry weight or water requirement. It also appears as seed-production and germination, the former being of the greatest significance with crop phytometers. When the impact of factors induces a qualitative change in growth, it results in adaptation, in terms of form or structure, or both, and this is definitely measurable, though it still lacks a proper system of units. Adaptation may likewise operate on the reproductive system, though less readily, and the flower affords further measures of the habitat, especially as to methods of pollination.

For the usual range of habitat measurements, the most serviceable phytometers are those for transpiration, photosynthesis, growth, and adaptation. The simplest, most convenient, and widely useful is the transpiration phytometer, as water-loss is the most variable and easily measured of functions. As the sum of all functions, growth furnishes the best single

phytometer of the total effect of habitat, while the difficulties of field application still leave something to be desired in the case of photosynthesis. For thoroughgoing and comprehensive investigation, the phytometer battery should contain plants assigned to each of the three determinations when these can not be safely carried out on each plant. This is necessary also for adaptation when the dry weight of plants is regularly determined.

NATURE AND RÔLE OF ZOOMETERS.

As members of the same community, animals resemble plants in that they can also be employed as measures of certain factors and relations. Because of their motility and the absence of the photosynthetic mechanism, they are much less affected by direct factors, with the exception of temperature. The latter is probably the most effective physical factor in the case of land animals at least, though the actual order of efficient factors must await quantitative physiological analysis. Even more controlling is the biotic factor of food-supply, and, in many cases, of materials and shelter. It is obvious that these can be directly measured, while the climate must at present be determined as a complex in which temperature and humidity are probably most important. In the case of burrowing and other soil animals it is probable that soil texture, aeration, and other factors may be measured to some degree. In aquatic habitats, which consist essentially of one medium, temperature, light, aeration, acidity, and salt-content are all susceptible of measurement.

Zoometers (ζῶον, animal; μέτρον, measure) may be distinguished on the basis of objective as climatic or factor, food, or pollination measures. The latter is obviously a food relation also, but of such a highly specialized sort as to deserve recognition. With respect to method, zoometers may be designated as indicator, transfer, and introduction. The first deals with the response of animals in the natural community, the second with the response in a new but related or adjacent habitat, and the third with that of domesticated or exotic animals. In all of these the method of exclosures and inclosures is fundamental. By the exclosure is understood an area fenced against all or selected species and with all or certain of the animals within it exterminated, while the inclosure is similarly treated, except that a certain number of animals are placed in it.

ESSENTIALS OF THE PHYTOMETER METHOD.

The fact that standard plants must be grown in sealed containers and placed in different and often extreme habitats demands that the species used should be as hardy and vigorous as possible. These requirements are usually best met by cultivated plants and weeds, and among native species by those of subruderal habit which readily invade bare areas. Because of the measurements required, species with simple entire leaves or large leaflets are to be preferred, such as the grains, sunflower, and bean. It is especially desirable that the individuals should be alike in size and form, and as uniform in response as possible. The latter can only be determined by preliminary readings, but this is imperative when each battery contains a small number of individuals. When there is a large number to select

from, those with a wide departure are rejected, but with a limited number, as is often the case with natives, the individuals are assigned to each battery in such a way as to give the same average response. Six constitutes an adequate number of individuals of each species when all are to be carried through, but 10 is better when short-period readings are also to be made. The number of species in a habitat battery will be determined by the results sought and the assistance available. In the case of standard plants used only for measuring transpiration or photosynthesis, a single species may suffice, but for comprehensive results 3 is a minimum, and 5 or 6 may be used to advantage.

The size of containers will be determined by several considerations, chiefly the size of the plants and especially the root systems, the region, and the help available. In the Pike's Peak region small containers are feasible because of the relatively low temperatures and short season and almost imperative because of the difficulties of transportation. In the Middle West, with long seasons and high temperatures, containers must be several times larger, 1 to 2 feet wide and several feet deep, to afford space for the roots. Since the containers must be impervious, tin, zinc, or galvanized iron is demanded. The seal presents greater difficulties, as it must shed rain, should not crack or injure the stem of the plant, and be capable of being applied with the minimum of time and expense. Much experimenting has been done in this connection, the outcome of which is given later. In the case of free phytometers the precautions to be taken are those indicated by the best nursery practice of the forester or florist.

While the number and location of stations will be determined by the problem, it is obvious that at least two are required for comparative values and that the habitats should show distinct differences in terms of indicators. Mountain regions afford peculiar opportunities for a climatic series because of the sharp gradient in a short distance, and seral habitats, as from pond to grassland or forest, offer the best range of edaphic conditions. The instrumental measurement of each habitat should be as complete as possible. The battery should regularly contain a hygro-thermograph, selagraph, anemometer, and rain-gage, and preferably a soil-thermograph and atmometer, and in addition, determinations of holard, soil-air, and solutes should be made whenever free phytometers are included in the series. Hygro-thermographs have been regularly placed in instrument shelters of the usual Weather Bureau type. The installation has been so organized that weekly visits suffice, at least for distant stations. The phytometers and instruments at each station are protected by a rodent-proof fence, but are fully exposed to the habitat above.

The major responsibility for the field work during 1918 was taken by Professors J. E. Weaver and F. C. Jean, and acknowledgment is also due Dr. Dolly Lutjeharms, Professor T. J. Fitzpatrick, Dr. Lee Bonar, and Mr. J. R. Bruff for their work during the other seasons.

CLIMAXES AND CLIMATES OF THE PIKE'S PEAK REGION.

Pike's Peak arises abruptly from the Great Plains at an altitude of 6,000 feet to a height of 14,142 feet, in a distance little more than 7 miles by airline. It is perhaps unique on the North American continent in this respect, as it also is in the fact that transport by rail is available for the entire distance. Moreover, its location below the thirty-ninth parallel in a great grassland climax with relatively low rainfall has permitted a greater differentiation of climates and climaxes on its slopes than is found on any other mountain of the continent. The region possesses the further advantage that quantitative studies in ecology were begun here in 1899 and have been carried on continuously since.

The visible zones from base to top are four, namely, grassland, chaparral, forest, and alpine meadow, but the forest zone comprises three climaxes. The series thus contains six climaxes, beginning with mixed prairie and extending through chaparral, woodland, montane forest, and subalpine forest to alpine meadow. The chaparral, consisting of *Quercus, Cercocarpus,* and *Rhus,* is much fragmented in this region and the woodland of *Pinus edulis* and *Juniperus* is near its northern limit, so that stations were not maintained in them after the first season.

MIXED PRAIRIE.

This climax receives its name from the fact that it comprises both tall-grasses and short-grasses, giving it a typical two-layered structure, in contrast to the other associations of the grassland formation. Over much of its area the tall-grasses have been much reduced or entirely removed by grazing, so that the community often consists of a low, usually dense cover of short-grasses belonging to the genera *Bouteloua* and *Bulbilis.* Of the dominants previously indicated for the mixed prairie and short-grass plains (Plant Indicators, pp. 135, 139), which are now regarded as the same climax, nearly all are to be found on the plains at the foot of the mountains. Of the tall-grasses the most important are *Stipa comata, Agropyrum glaucum,* and *Sporobolus cryptandrus,* while the chief short-grass is *Bouteloua gracilis* (plate 2A). *Bulbilis dactyloides,* the regular codominant of the latter to the eastward, is here found only in occasional playa-like depressions. The postclimax Andropogons, *A. scoparius, furcatus,* and *nutans,* are often abundant and sometimes dominant in areas with higher holard, such as valleys, mesas, and stable sandhills. The number of subdominants is nearly as great as in the true prairies, but the individuals are less abundant and luxuriant, and the societies much less mixed. The most widespread societies in the spring are *Aragalus lamberti, Sophora sericea,* and *Senecio aureus,* of the summer *Psoralea tenuiflora, Lepachys columnaris,* and *Haplopappus spinulosus,* and of the autumn *Artemisia frigida* and *campestris, Gutierrezia sarothrae, Grindelia squarrosa, Liatris punctata,* and *Carduus undulatus.*

The climax stage occupies more than nine-tenths of the area. The hydrosere is limited to a few artificial ponds and lakes, characterized chiefly by the *Scirpus-Typha* associes, while the xerosere is confined to the cliffs

and talus of the mesa escarpments. Subseres are found primarily in sandhills and sandy plains, and to some extent in fallow fields and overgrazed pastures. The former are chiefly in the subclimax stage marked by *Andropogon halli* and *scoparius* and *Artemisia filifolia*, often with much *Calamovilfa longifolia* and *Elymus canadensis*. The first climax grasses to enter are usually *Sporobolus* and *Stipa*, followed by *Bouteloua*. Overgrazed areas are characterized by the absence of the tall-grasses and the increasing abundance of *Muhlenbergia* or *Aristida*, and in the later stages by the dominance of *Artemisia frigida* or *Gutierrezia*, or by both.

The rainfall is approximately 15 inches in this portion of the climax, with an amplitude of 8 to 22 inches. The mixed prairie is chiefly in contact with the chaparral, which breaks up into numerous miniature groves over an ecotone often one to several miles wide. However, the broken topography and the cyclic variation in rainfall bring the grassland also in contact with the woodland and the montane forest, with which it forms characteristic and extensive savannah at altitudes of 6,000 to 7,000 feet.

MONTANE FOREST.

This climax is a coniferous forest extending generally from 7,000 to 9,000 feet. The major dominants are *Pinus ponderosa, Pseudotsuga mucronata*, and *Abies concolor*, with *Picea pungens* and *Pinus flexilis* scattered or locally prominent (plate 2B). In this region the three dominants practically never meet on equal terms, *Pinus* taking the drier warmer slopes and *Pseudotsuga* and *Abies* the moister cooler ones. However, they do mix sufficiently to prove that there is no climax difference between them. The yellow pine forms pure stands in the lower portion of the zone, the white fir in the middle, and the Douglas fir in the upper part, the last two often making a mixed forest also. Fire has occurred more frequently in the open canyons, and these have come to be occupied by open aspen forest with a striking herbaceous undergrowth, consisting of *Geranium, Calochortus, Campanula, Pentstemon, Rudbeckia, Valeriana*, etc. Societies are much less developed in the climax forest, the primeval portions often containing only scattered clans of shade forms and saprophytes. Among the most important subdominants of the typical forest are *Mertensia, Thalictrum, Chamaenerium, Castilleia, Erigeron, Zygadenus, etc.* (Plant Indicators, 207).

About a third of the area of the montane zone is covered by the climax, another third by aspen, and the remainder by seral communities. The hydrosere is little in evidence, and the subsere is represented almost wholly by the burn succession. The rock xerosere is much the most important, the stages most in evidence being the gravel-slide of bunch and mat herbs and the half gravel-slide dominated by grasses. The grass and scrub stages are best developed on the southerly slopes, and are composed chiefly of dominants from the chaparral and mixed prairie that migrated upward during the dry phase of the climatic cycle. At its upper edge the montane forest lies in contact with the subalpine climax, while below it is usually in touch with woodland, though it frequently meets chaparral and grassland also. The average rainfall is about 21 inches, with an amplitude of 15 to 26 inches. Two-thirds of the total falls between April 1 and August 31, as

is likewise true of the glassland climax, owing to the summer type of precipitation.

SUBALPINE FOREST.

This is a coniferous forest resembling the preceding in many respects, but consisting of a single great dominant in the Pike's Peak region. While the Petran subalpine climax is regularly constituted by *Picea engelmanni* and *Abies lasiocarpa*, the latter is lacking here and the forest is pure for the most part, *Pinus aristata* becoming more or less abundant as timber-line is approached and *P. flexilis* appearing along rocky ridges (plate 3A). The lodgepole pine, *P. contorta*, which covers much of this zone northward as a burn subclimax, is also absent, and the extensive burns are covered with aspen in consequence. The societies of the forest floor resemble those of the montane climax, belonging to the same genera for the most part, but are less dense and luxuriant in consequence of the shorter season (Plant Indicators, 224).

The annual rainfall is approximately 25 inches, with an amplitude of 18 to 33 inches, and the mean temperature 36° F. The greater rainfall and smaller evaporation make lakes and ponds more numerous, and the hydrosere is best represented in this climax. The submerged and floating stages are little developed, and the amphibious ones are represented only by sedges and rushes. The latter may be followed by a wet-thicket stage of *Betula* and *Salix*, or it may pass directly into the grass stage on better-drained soil. The xerosere is confined to cliffs, talus, and gravel-slides, with the stages more or less fragmentary.

ALPINE MEADOW.

The alpine zone is occupied by a climax composed of sedges and grasses, for the most part but a few inches high. The major dominants are *Carex rupestris* and *filifolia*, while a large number of species of *Carex* and *Poa* play some part. This climax recalls the true prairie in the large number of bright-flowered subdominants, which are its most notable feature. It extends from 11,000 feet to the tops of the highest peaks, above 14,000 feet, though the lower limit varies much with the exposure. As fire and grazing have affected this community but little, the subsere is practically absent, except for small disturbed areas due to mining or water-supply operations. Owing to the relatively high rainfall, very low evaporation, and short season, lakes and swamps are abundant. Submerged and floating plants are rare, however, and the hydrosere consists of few stages, the most characteristic being the sedge and thicket communities. The xerosere is likewise simple, its most typical stage being marked by cushion-plants, such as *Silene acaulis, Androsace chamaejasme, Arenaria sajanensis*, and *Paronychia pulvinata* (Plant Indicators, 232).

The rainfall on Pike's Peak is 30 inches, with an amplitude of 9 to 44 inches, a little more than half of which occurs in the summer. The mean temperature is 19° F., 17° lower than for the subalpine zone, and 31° lower than for the mixed prairie.

METHODS AND RESULTS, SEASON OF 1918.

Two stations were installed for the first two series in 1918 and continued for the third. The plains station was located about 5 miles east of the base of the range, at an altitude of 6,150 feet. The ground is comparatively level, sloping to the south about 2°. An inclosure 30 by 10 meters was fenced against cattle by means of barbed wire, and a portion of this was protected against rodents by means of coarse woven-wire reinforced by screen. The montane station was established on the south wall of Engelmann Canyon, at an altitude of 8,600 feet. The slope-exposure is about 30° to the north. The area was covered with a young stand of Douglas fir and aspen, which was cleared for a space 10 meters square to remove the shade. The experimental area was inclosed with wire screen 6 dm. wide and of 2 mm. mesh, and the exclusion of rodents was made complete by sinking the screen 1 dm. in the ground and bending the upper edge down obliquely (plate 5).

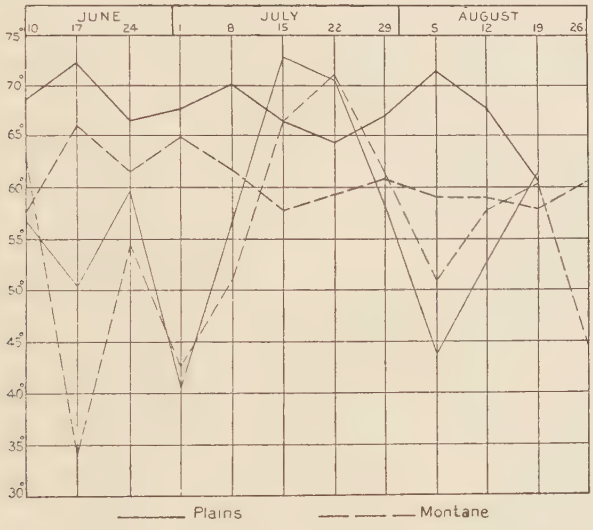


FIG. 1.—Average temperature (heavy lines) and humidity (light lines), 1918.

For the third series three additional stations were established. The gravel-slide station was installed on the exposed northwest slope of a ridge about 100 meters above the montane station. The decomposed granite of the gravel-slides constitutes the most xerophytic habitat of the montane climax, with the exception of cliffs and rock surfaces. The seral stage characteristic of it consists of bunch and mat herbs, such as *Aletes, Aragalus, Eriogonum,* etc., and the edges are marked by dwarfed individuals of *Pinus flexilis.* The Douglas-fir station was located on a northerly slope at an elevation of 8,600 feet, in the midst of the climax association of *Pseudotsuga mucronata,* and the Engelmann-spruce one in climax *Picea engelmanni* of the subalpine forest, at an altitude of 9,000 feet. No clearing was made in connection with the last two, but protection against rodents was provided in the usual manner.

The species used as standard plants for the three series of phytometers in 1918 were sunflower (*Helianthus annuus*), pinto beans (*Phaseolus vulgaris*), Kherson oats (*Avena sativa*), Marquis spring wheat (*Triticum sativum*), sweet clover (*Melilotus alba*), and wild raspberry (*Rubus strigosus*). The seeds of the five cultivated plants were germinated in flats after soaking for 12 hours in warm water, while young plants of raspberry were transplanted from nature. The same soil was used throughout the series, consisting of a reddish sandy loam obtained from a garden in Manitou. The analyses of this soil gave the results shown in table 1.

TABLE 1.—*Phytometer soil.*

Mechanical analysis.		Chemical analysis.	
Coarse gravel	7.1	P_2O_5	0.208
Fine gravel	0	SO_3	0.0014
Coarse sand	15.6	K_2O	2.36
Medium sand	12.3	Fe, Al, Ti, oxids	(–)
Fine sand	29.3	CaO	(–)
Very fine sand	20.0	MgO	(–)
Total sand	77.2	SiO_2	(–)
Silt	14.0	Nitrogen	0.130
Clay	8.8	Volatile matter	3.50
Hygr. coef	5.7	Acidity	0
Wilt. coef	8.4	HCl test	0
Moist equiv	15.4		
Max. water-content	45.8		

The containers were chiefly cylindrical vessels of galvanized iron, approximately 6 inches wide by 14 inches deep. The soil used was run through a sieve of ¼-inch mesh and moistened to a condition of good tilth, being worked by hand to insure uniform distribution of the water. About 2 cm. of coarse gravel was placed in the bottom of each container for a water reservoir, and a glass-tube 1 cm. wide so adjusted that the lower end extended into the gravel, while the upper stoppered end reached just above the rim of the container. The latter was then filled almost to the top with the soil, which was firmly compacted in the process. The dicotyl seedlings were transplanted about the time the cotyledons appeared, a single one being placed in the center and carefully thrust through a hole 1 cm. in diameter, bored in a large flat cork used as a stopper. This was then sealed by means of a wax consisting of 85 per cent paraffin and 15 per cent petrolatum, which was poured over the soil surface and spread evenly by tilting the container from side to side. The opening in the cork around the stem was next filled with a fine, dry dust-mulch, which prevented evaporation but allowed the stem to grow under fairly normal conditions. The cereals were treated in the same manner, except that five germinating seeds were placed in a slit 1 by 4 cm. cut in the cork stopper. This slit was then partly filled with moist soil before applying the dust-mulch.

The containers were sunk in the soil of the station at which they were to be grown, so that the tops were slightly above the surface. To insulate them from the extremes of surface temperature, as well as to facilitate their removal for weighing and watering, each container was surrounded by a

collar of the same height, but 1 inch greater in diameter. To serve as a further insulator and to prevent the softening of the wax during the heat of the day, the containers were covered with a doubled thickness of woollen blanket, over which was placed an oil-cloth one covered with a centimeter or more of soil, a slit permitting the stem of the plant to protrude. Each plant was thus sealed in the container without the stem being touched by the wax; the container was below the soil surface but separated from it by an air-jacket, and was protected from the heat of the sun by triple insulation.

At intervals the containers were removed and weighed, and the original weight restored by the addition of water through the glass tube. At the close of each series all phytometers were weighed and the plants cut at the level of the soil surface. Blue-prints were at once made of the leaves and the areas determined later by means of the planimeter, and dry weights were obtained in the usual fashion. The physical factors were recorded throughout the season by means of standard apparatus. Humidity and air-temperature were determined by means of Friez hygro-thermographs, rainfall and wind by the Weather Bureau rain-gage and anemometer, and evaporation by the Livingston porous-cup atmometer. In addition, occasional series of simultaneous readings were made at the various stations to determine comparative soil-temperatures. Measurements of the holard were made at all stations at various depths, though these did not bear directly on the phytometers, in which the water-content was under control. In order to obtain the average temperature and humidity for the week at each station, the value at each of the 12 points in each 24-hour day where the curve intersects the 2-hour line of the record sheet was taken and averaged. The weekly average for temperature or humidity was thus obtained from 84 readings taken at 2-hour intervals throughout the week. Similar averages were obtained for day and night values, using the 2-hour readings from 8 a. m. to 6 p. m. for the day and from 8 p. m. to 6 a. m. for the night.

Temperature.

The decrease of air-temperature with the altitude is exemplified by the summer averages for the plains and montane stations. For the 24-hour day the drop is 7°, while it is nearly a degree greater for the day and about 2° less for the night. The greatest differences were found in June, when one week gave decreases for the montane station of 16° for the 24-hour period, 10° for the night, and 21° for the day. These results are in general accord with those obtained from 1903 to 1905, when an average difference of 10° was found to exist between the plains and the montane zone. As would also be expected, the plains exhibited a greater range of temperature in the 24-hour period, this being reflected in an average range of 18° in contrast to 15°. The temperature at 3 inches above the soil-surface decreased more or less regularly with the altitude for the five stations from the plains to spruce forest, though exposure and cold-air drainage reversed the relation in the morning to some degree (fig. 1).

In the case of soil temperature, there is likewise a marked decrease with altitude, influenced more or less by exposure and to a marked degree by

cover, as well as by depth of reading. At a half inch below the surface the average difference during the afternoon was more than 10°, while at a depth of 4 inches it was 7°. At the surface there was a difference of 17° between the montane station and those in Douglas fir and Engelmann spruce, due chiefly to the removal of the cover in the former, while at a depth of 2 feet the difference had dropped to 5° (fig. 1).

Humidity and Evaporation.

The average relative humidity differed but little between the two stations, being 56 per cent on the plains and 54.7 per cent in the montane zone. During the day, when humidity is most efficient, it was nearly 4 per cent less on the plains and at night it was 7 per cent greater. The daily variation

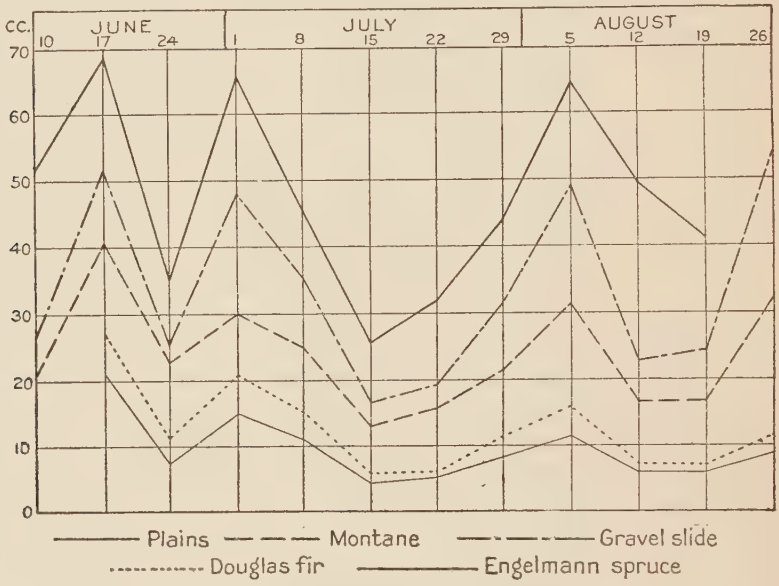


Fig. 2.—Average standard evaporation, 1918.

was much greater at the plains station, namely, 21 per cent, in contrast to 10 per cent (fig. 1). As to wind movement, the plains led with a daily average of 120 miles, the gravel-slide was second with 103 miles, the montane station third with 67 miles, and the Douglas-fir station last with but 29 miles, a result readily explained by the forest cover.

Evaporation was obtained by means of standardized, white, cylindric atmometer cups set on non-absorbing mounts, placed in the soil in such manner as to bring the evaporating surface on a level with the phytometers. The plains station yielded a daily average of 47.8 c. c., twice as great as that for the montane station, namely, 23.7 c. c. The xerophytic gravel-slide was nearly intermediate, 33.9 c. c., while the two forests were respectively 13 and 9.6 c. c., approximately half that of the open montane station in the same general altitude (fig. 2).

Summary.

The plains station exhibited the highest and most variable temperatures of air and soil, the most variable holard, and the greatest average wind

movement. In the order of decreasing temperature the other stations were the gravel-slide, montane, Douglas fir, and Engelmann spruce. The latter station gave the highest rainfall and holard and the lowest average temperature. Rainfall was lowest and wind and evaporation highest at the plains station, and the last two decreased through gravel-slide and montane to Douglas fir. On the basis of the usual indirect factors, the relative humidity should be consistently lower at the plains, but these were partly offset by the effect of altitude and of cold-air drainage at night.

Phytometers, First Series.

After soaking 12 hours in warm water, a quantity of sunflower seeds was planted in small pots of garden soil at the montane station on June 7. Twelve of the most vigorous individuals were transplanted into sealed containers at this station on June 13, and on the next day an equal number of similar plants was transferred to the plains station. They were sunk in the soil here and repotted on the 17th in sealed containers without disturbing the root system. Pinto beans were first grown in pots in the same way, and then placed in sealed containers at the montane station on the morning of June 17 and at the plains station during the afternoon of the same day. After the usual soaking, wheat and oats were planted directly in sealed containers at the former on June 15. At the same time an equal number were planted in small pots, from which they were transferred to containers at the plains station on June 18, when only a few plants had appeared above ground.

Owing to losses, caused chiefly by grasshoppers, the original number of plants, 6 at each station, was carried through the series only in the case of beans. The sunflowers were reduced to 9 (4 plains and 5 montane), the oats to 7, of which 2 were plains and 5 montane, and the wheat to 3, one plains and 2 montane. Soil samples taken in duplicate gave the following holards for the various species and stations: plains station, wheat, oats, and sunflowers 25.9 per cent and beans 24.7 per cent; montane station, wheat and oats 23 per cent, sunflowers 22.6, and beans 25.2 per cent, indicating that the water-supply was essentially identical for all.

Readings.

The average transpiration per unit of leaf-area was much larger for the plains than for the montane station. For the sunflowers the average water-loss per square decimeter of leaf was 376 c. c. and 264 c. c. respectively, while for beans it was 408 c. c. and 238 c. c. Stated in percentages, transpiration at the montane station was 70 per cent of that at the plains in the case of sunflowers and 58 per cent in the case of beans. The individual variation of the sunflowers was small, being but 5 per cent for the plains and 7 per cent for the montane plants. There was no effective difference in leaf-area between the two stations (table 9).

The plants of this series were cut July 10, and the dry weights obtained by drying to a constant weight at 100° C. The average dry weight was slightly greater at the montane than at the plains station for sunflower and beans, while it was much higher at the latter for oats and wheat (plate 4).

On the basis of the plains values the percentages at the montane station were 101 for sunflowers, 103 for beans, 65 for oats, and 91 for wheat. The water requirement as defined by Briggs and Shantz, namely, the amount of water used in the production of 1 gram of dry material, was highest at the plains station for all the species employed. The average water requirements for plains and for montane were respectively 518 and 370 for sunflower, 542 and 365 for beans, 765 and 509 for oats, and 766 and 657 for wheat. In comparative terms the sunflowers required 71 per cent, beans 67 per cent, oats 66 per cent, and wheat 86 per cent as much water at the montane as at the plains station, these figures agreeing with those for transpiration above (table 9).

Phytometers, Second Series.

The second series of phytometers differed from the first chiefly in being carried through a longer period of growth, namely, until the 22d of July instead of the 10th. The method employed was essentially the same, except that only 2 sealed phytometers of each of the four species were used, and sweet clover (*Melilotus alba*) was substituted for beans. To disclose any possible ill effects of sealing, unsealed phytometers were placed at each station and given the same treatment as the sealed ones. In these, however, beans replaced sweet clover. Thus, both stations were provided with 8 sealed phytometers, making 2 each of sunflower, wheat, oats, and sweet clover, while the plains station had 16 and the montane 15 unsealed phytometers.

Readings.

As in the first series, the average transpiration per unit area was much greater at the plains station, being practically twice as much. Thus, for sunflowers the water-loss was 508 c. c. at the plains and 252 c. c. at the montane station, for oats 367 c. c. and 162 c. c., and for wheat 386 c. c. and 197 c. c. respectively. The transpiration at the montane station was 50 per cent of that on the plains for sunflowers, 44 per cent for oats, and 51 per cent for wheat. The individual variation was again low for the sunflowers, being 1 and 6 per cent, but it was much higher for the cereals. The leaf-area of both sunflowers and wheat was greater for the montane region. The sunflowers in unsealed containers showed a much smaller leaf-area at both stations than those in sealed containers, indicating that sealing did not affect growth unfavorably. The relations with respect to the average dry weight were the reverse of those for the first series, the values being higher at the plains station for sunflower and sweet clover, and higher at the montane for oats and wheat. On the basis of the plains results, the percentages at the montane station were 81 for sunflowers, 62 for sweet clover, 166 for oats, and 230 for wheat (tables 9 to 12). The water requirement was again higher at the plains station, for the sunflowers being 382 as against 285 for the montane station, for oats 536 to 335, for wheat 486 to 320, and for sweet clover 529 to 300. The requirement at the latter was 74 per cent for sunflowers, 63 per cent for oats, 66 per cent for wheat, and 57 per cent for sweet clover of that at the plains station, agreeing closely with the figures for the first series, except in the case of wheat. It is somewhat

surprising to find that the water requirement is less than in the first series, in which the plants were cut 12 days earlier.

Phytometers, Third Series.

Three species were employed as phytometers in this series, namely, sunflower, oats, and wild raspberry (*Rubus strigosus*). While the methods of planting and sealing were the same, the soil was a mixture of that previously used with one-fourth as much fine gravel. The holard was 18 per cent in all cases. Two or three sealed phytometers were carried through the series at the five stations, and unsealed checks of sunflower and oats were also located at each. All of these were installed July 10 and removed August 16.

Readings.

The average transpiration for all three species was greatest at the plains station with 970 c. c. for sunflower, and it decreased through the stations with the following order and values: gravel-slide 320, montane 310, spruce 169, and fir 142. In the case of oats the values were respectively 510, 390, 335, 69, and 28, and for raspberry 401, 249, 230, 97, and 65. On the basis of the plains station the water-loss of sunflowers was, respectively, 33, 32, 17, and 15 per cent, of oats 76, 66, 14, and 6 per cent, and of raspberries 62, 57, 24, and 16 per cent. As to leaf-areas, these were greatest for oats and raspberries in the plains and least at the Engelmann-spruce and Douglas-fir stations, while the sunflowers gave the greatest area in the montane and gravel-slide stations for the sealed phytometers, the results in the unsealed ones diverging somewhat (tables 9 and 12).

The average dry weight of sunflowers was greatest at the montane station, 2.5 gm., less at the gravel-slide and plains stations, 1.9 and 1.6 gm., respectively, and least at the spruce and fir stations, 0.36 and 0.31 gm. As percentages based on the plains station the values were 152 per cent for the montane, 118 for the gravel-slide, 22 for the spruce, and 19 for the fir, while for the unsealed checks they were respectively 93, 48, 9, and 7 per cent. In the case of oats, on the other hand, the relation of sealed and unsealed phytometers was reversed. For the sealed ones the results were 82 per cent for the montane, 62 for the gravel-slide, 20 for the spruce, and 13 for the fir, while the unsealed yielded, respectively, 132, 117, 55, and 42 per cent.

As in the other series, the water requirements were highest at the plains station and decreased with altitude and shade. For the sunflowers the averages were as follows: plains 1,140 c. c., gravel-slide 489 c. c., montane 372 c. c., fir 321 c. c., and spruce 316 c. c., while the oats gave 893, 575, 535, 156, and 320 c. c., respectively. Expressed in per cent of the plains values, the figures are 43, 33, 28, and 27 for sunflower, and 64, 60, 17, and 36 for oats (tables 9 to 12).

Summary.

The results of the three series are summarized in tables 10 and 12, and from these the following conclusions may be drawn:

1. The water requirement of sunflowers is greater at the plains than at the montane station. The order of decreasing value when other stations were represented is plains, gravel-slide, montane, fir, and spruce. The same

relation is true of beans, wheat, and sweet clover where these were used, and also for oats, except that the fir and spruce stations are reversed.

2. Essentially the same sequence holds for the transpiration per unit of leaf-area, both for the cultivated species and the native *Rubus*, as for water requirement.

3. The relation shown by water requirement and transpiration is similar to that found for temperature and for the evaporation from the porous-cup atmometer.

4. In regard to growth the response was less uniform, as shown both by dry weight and leaf-area. Sunflowers and beans usually made the best growth at the montane station, but in the longer second series the sunflowers were larger at the plains station. In the case of the other species the individuals at the plains were usually somewhat larger, though the second series furnished an outstanding exception in favor of the montane habitat. The discrepancies are probably to be explained by differences in the total requirements of the species and by diverging changes in the factor-complex with the advancing season.

5. The comparison of behavior and growth in sealed and unsealed containers shows that presence of the seal had no unfavorable effect.

METHODS AND RESULTS, SEASON OF 1919.

Three climax stations were maintained during the season, the plains and montane stations being continued as for 1918. The third one was established in the subalpine climax of Engelmann spruce (*Picea engelmanni*) at an altitude of 10,800 feet. It was located on the top of a ridge along the east slope of Pike's Peak, formed by the terminal moraine of an old glacier. The ground sloped about 7° to the northeast and was strewn with large boulders. The spruce trees are small and scattered in an old burn, their size being partly due to the proximity of timber-line, which is but a few hundred feet higher at this point. The burn is now largely covered with grove-like communities of aspen. The experimental area was fenced with wire screen in the manner already described. Owing to the open nature of the community, it was unnecessary to effect a clearing in order to expose the phytometers to the sun (plate 3A).

The detailed methods were essentially the same as those employed in 1918. The containers used for both series were of sheet-metal, and were approximately 16 cm. wide and 20 cm. deep. The soil was practically identical with that used in the previous year, being taken from the same spot and treated in the same fashion. The seed was obtained from the same source as before, and was germinated and the plants transferred, sealed, and cared for as already described. The treatment of the containers differed only in the fact that no collars were used, the soil being in contact with the pails and thus necessitating careful wiping and drying before they were weighed.

Hygro-thermographs were installed in standard shelters at the plains and montane stations, the readings being checked each week by standard thermometer and psychrometer. Owing to various vicissitudes it proved impossible to place one of these instruments at the subalpine station, but a thermograph was added later, and psychrometer readings were taken from time to time. Standardized porous-cup atmometers were run in duplicate at each station inside the phytometer inclosure, the cups being set at the approximate level of the leaves. The results in all cases have been corrected to the standard and the average of the two readings used. The rainfall was recorded for each station, and the holard was determined to a depth of 3 feet each week and to 4 feet at the plains station at least once a month.

Temperature.

The air-temperature decreased with the altitude as for the previous year, but this fact was somewhat obscured by the greater effect of cold-air drainage. However, the difference in the day average for the plains and montane was much less, owing to several inversions, in spite of the fact that the curves (fig. 3) show the plains to be usually about 5° higher. Since the average for the plains at night is actually lower, there is indicated no efficient difference in the 24-hour average for the two stations. The usual relation is much more clearly revealed by the temperatures of the subalpine station where the results are not disturbed by the effect of air drainage. For all three periods they are 10° to 12° higher than for the montane region,

as instrumental studies had shown two decades earlier. The plains exhibit a somewhat greater daily range, being warmer by day and cooler at night than the montane region.

Humidity and Evaporation.

The relative humidity at the montane station was 10 per cent higher than at the plains station for the summer average during the day, while the night humidity was 17 per cent lower. The latter was partly due to cold-air drainage, but chiefly, it would seem, to two weeks of unusually high humidity on the plains. Since the day humidity is several to many times more efficient than night humidity in controlling transpiration, owing to stomatal behavior, the plains are really drier in effect, in spite of the fact that the 24-hour average for the montane region is 3 per cent lower. This is also attested by the greater evaporation (fig. 4).

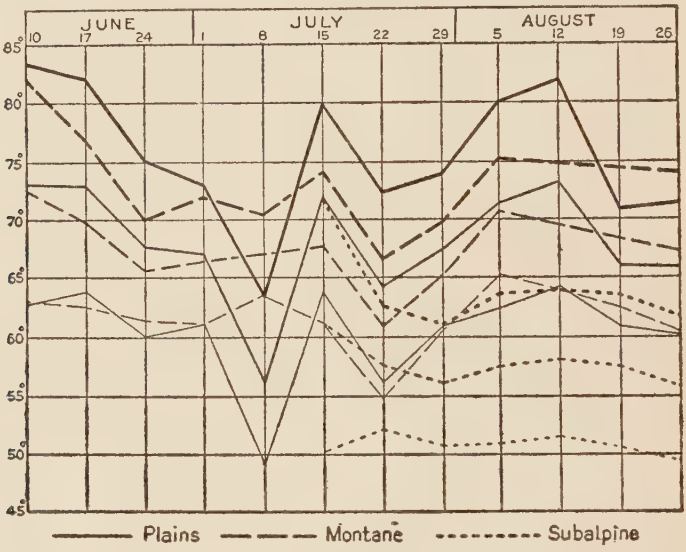


Fig. 3.—Average temperature for day (heavy lines), 24-hours (medium lines), and night (light lines), 1919.

Evaporation was highest at the plains, intermediate at the montane, and lowest at the subalpine station, the daily averages for the season being respectively 32, 30, and 20 c. c. The curves for the season (fig. 5) show that the plains evaporation is often much higher than for the montane zone, while that for the subalpine zone is regularly much lower.

Summary.

For the season of 1919, the plains station exhibited the highest and most variable average air-temperature, the highest average soil-temperature and holard, a slightly higher relative humidity, and the highest evaporation. The montane station was intermediate in average air and soil temperature and evaporation, slightly lower in relative humidity, and lowest in holard. The subalpine station gave the lowest and least variable average air-tem-

perature, lowest soil-temperature and evaporation, and an intermediate holard.

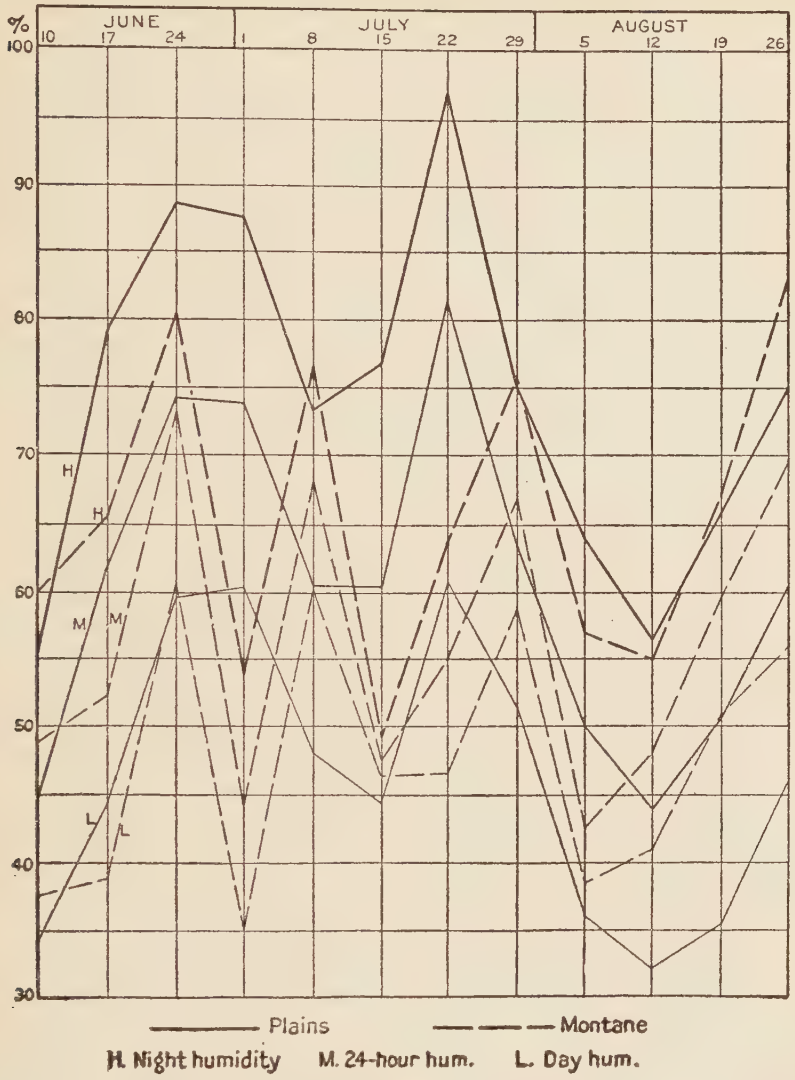


FIG. 4.—Average humidity for day (heavy lines), 24-hours (medium lines), and night (light lines), 1919.

PHYTOMETERS, FIRST SERIES.

Four species were employed in this series, namely, sunflower, pinto beans, Marquis spring wheat, and Kherson oats. Five sealed and an equal number of unsealed phytometers were maintained at each of the three stations. All these were planted between June 24 and 27, the grains after a few days' growth in germinators and the others after the expansion of the cotyledons. Both sunflower and beans were planted in flats and grown in the greenhouse

from June 16 until they were transferred to the containers. The holard of the soil varied from 18.5 to 22 per cent. All plants were removed on August 1, blue-prints were made of the leaves, and the green and dry weights were obtained in the usual manner.

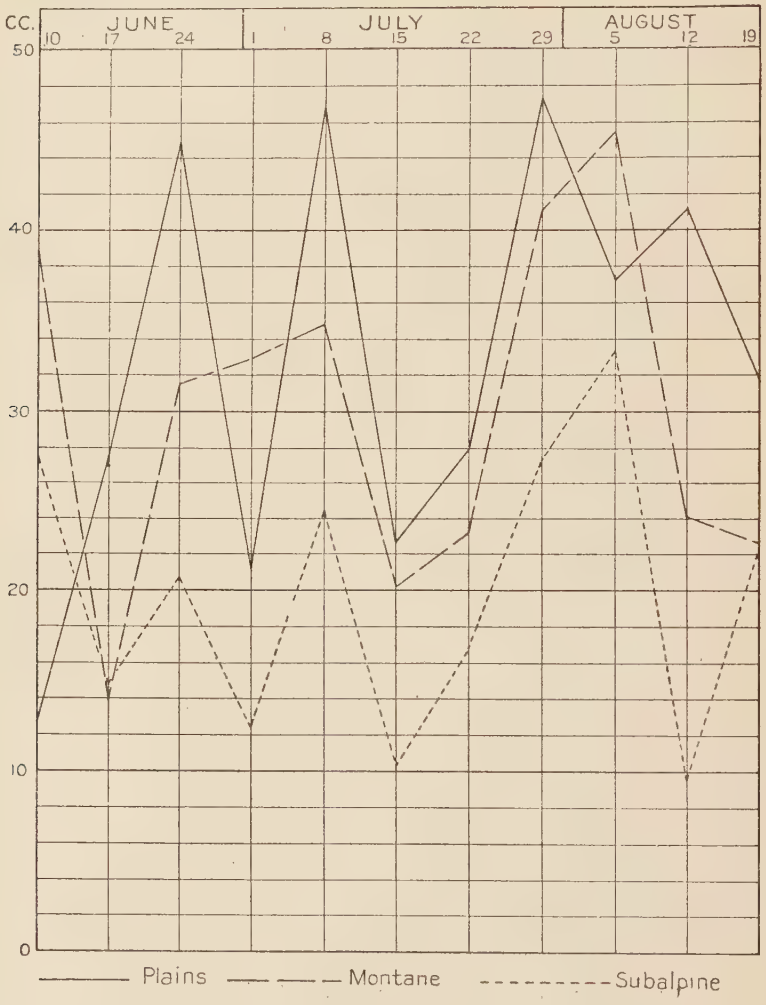


FIG. 5.—Average evaporation, 1919.

READINGS.

Transpiration per unit of leaf-area agreed with the results of the preceding year, being greatest at the plains station and decreasing rapidly with the altitude. This is well illustrated by the sunflower, in which the transpiration fell about 200 c. c. for each station, namely, from 644 c. c. to 425 c. c. and 230 c. c. The sunflowers gave 65 per cent at the montane station and 35 per cent at the subalpine of the water-loss at the plains, while for wheat the values were 58 and 20 per cent, for oats 44 and 37 per

cent, and for beans 58 and 56 per cent. The response as to leaf-area appears to have been influenced by the heat requirements of the species, since the leaves of sunflower and bean were largest at the plains station, and those of wheat and oats at the montane. Moreover, the area at the subalpine station was less than half for sunflower and less than a seventh for beans of that at the plains, while for both wheat and oats it was greater, being only a little less than in the montane zone (table 13).

The growth of the plants, as indicated by the dry weight, is in complete accord with the results for leaf-area, though the figures are even more striking. The dry weight of sunflower and bean was greatest at the plains, and that of wheat and oats in the montane region. For the first two it was reduced approximately 50 per cent for each station, being 12 gm. at the plains and 3 gm. at the subalpine station for the sunflower, and 5.8 gm. and 0.8 gm. respectively for the bean. For wheat, the montane value was 2.57 gm., the subalpine 1.76 gm., and the plains 1.60 gm., while for oats the respective figures were 1.72, 1.63, and 1.25. The green weights are in general agreement with the dry weights, the ratio between the two indicating that the plants became more succulent with increasing altitude, a fact already established by observation.

As established by the 1918 series, water requirement decreased with the altitude. For sunflower and beans the respective values were 401 and 665, 352 and 424, and 280 and 287; for wheat and oats, 557 and 567, 351 and 342, and 173 and 249. On the basis of the plains requirement, sunflower needed 87 per cent as much water in the montane climax and 72 per cent in the subalpine, while wheat required 68 and 26 per cent respectively. The relative requirement was much the same for oats and beans in the montane region, namely, 59 and 63 per cent, as it was likewise for the subalpine zone, 43 and 47 per cent. Thus, while all species decreased their requirement with increasing altitude, sunflower made the least reduction and wheat the greatest. The general correspondence in the water requirements of the four species at the montane station is significant of its intermediate position between the limiting effect of heat and dryness on the plains and cold in the subalpine climax.

Phytometers, Second Series.

Three sealed and three unsealed phytometers of each of the three species, sunflower, Marquis spring wheat, and Kherson oats, were employed at the various stations for this series. An accident at the plains station left but two sunflower and two wheat phytometers there. In addition to these, two wheat phytometers, sealed by the method used in 1918, were run at each station, as well as three unsealed ones of each species as checks. Three additional checks were grown in soil placed in trenches alongside the regular containers to determine the effect of the limited size of the containers on the plants grown in them. Results for these are not included in the tables, since they gave practically the same green and dry weights as the plants in containers. It appears certain from this and other tests that the containers exerted no limiting effect on growth for the relatively short period of each series.

Readings.

Transpiration again decreased with the altitude in the case of both sealed and unsealed containers, with the exception of the sealed wheat checks at the plains and the sealed oats at the subalpine station. It decreased more rapidly with sunflower than with wheat or oats, and more rapidly with the unsealed than the sealed phytometers. The average water requirement showed a constant decrease from the plains to the montane and subalpine stations, with the exception of oats at the second, where the high value results in an inexplicable discrepancy. The results as to growth in terms of leaf-area and dry weight vary so much from those obtained in preceding series as to indicate an exceptional irregularity in the conditions of growth for the different species at the various stations (tables 13 and 14).

Summary.

1. Transpiration decreased with the altitude in both series, being greatest on the plains and least in the subalpine zone.

2. Water requirement likewise decreased with the altitude in both series.

3. Growth was regularly best for temperate species, sunflower and beans, at the plains station, while for boreal ones, wheat and oats, it was usually best at the montane station.

METHODS AND RESULTS, SEASON OF 1920.

The same three stations, plains, montane, and subalpine, were maintained in 1920 as for the previous season, no alterations that could effect conditions being made. Three species were used through the season, during which two series of phytometers were run, comprising sunflowers, Marquis spring wheat, and Kherson oats. The seed was obtained from the same source as that used in former years and was as nearly as possible identical with it. Soil, containers, methods of handling the plants, and sealing were precisely the same as described for the second series of 1919. Five sealed and five unsealed plants of each species were installed at each station. In addition to these, three phytometers in large containers 4.5 dm. deep by 3 dm. in diameter were planted with wheat at both the plains and montane stations, two of each battery being sealed in the same way as the smaller containers, while the third was left unsealed as a check. The results for these large containers are given at the end of the other phytometer data, as they were run in but one series.

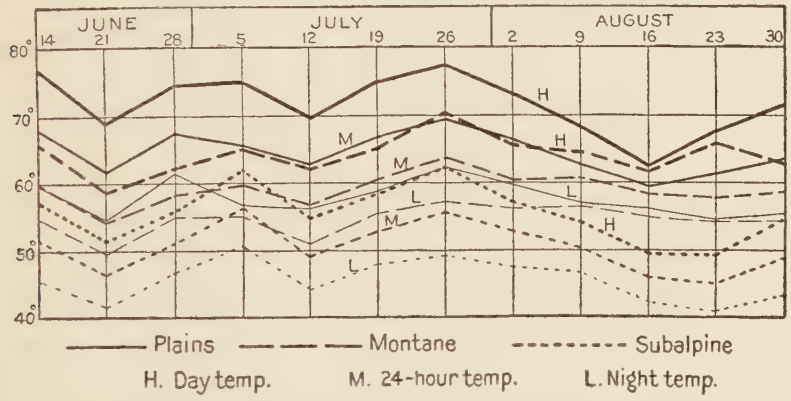


FIG. 6.—Average temperature for day (heavy lines), 24-hours (medium lines), and night (light lines), 1920.

Hygro-thermographs were operated at each station in standard shelters placed on the ground close to the experimental inclosures. The instruments were checked weekly by duplicate thermometer and psychrometer readings. In case of an error of 5 per cent or more, as occasionally happened with the hydrograph, the averages given in the table were obtained by integration. Standardized white cylindrical atmometers with non-absorbing mounts were run in duplicate within each inclosure and so placed as to bring the evaporating surface as nearly level with the leaves as possible. As in the case of those for the previous season, the results are averages based on weekly readings of the two instruments. An anemometer was placed in each inclosure and the cups brought to a height of 12 inches above the surface of the ground to get as nearly as possible the conditions of wind to which the leaves were exposed. Rain was recorded at each station, and the holard at various depths was determined weekly.

Temperature.

In average temperature for the season, the plains station is highest, the montane second, and the subalpine lowest, the averages for the season

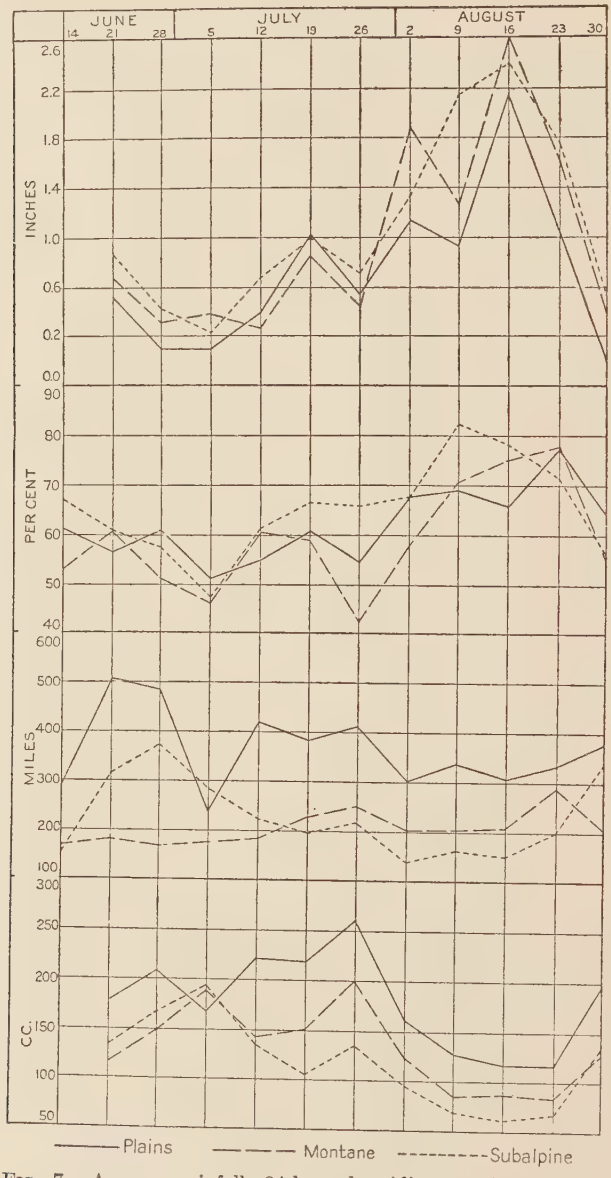


Fig. 7.—Average rainfall, 24-hour humidity, total wind, and average evaporation, 1920.

being respectively 64.5°, 59.1°, and 50.5° (fig. 6). The curves of the 24-hour averages for the period show plainly a relation through the summer similar to that indicated by the summer averages. There is a close agree-

ment between the variations in temperature at the three stations, especially during the first part of the season, corresponding with the first series of phytometers, while during the second series the subalpine temperatures show a decline, indicating the early approach of autumn at the higher altitudes. The averages yield the same relation, viz, plains stations 65.4° and 63.7°, montane station 58.3° and 59.9°, and subalpine station 51.3° and 49.7° for the first and second series respectively. The day averages for the plains station are relatively high. Thus, the results for the time of the first series show a difference between the day average at the plains (73.2°) and at subalpine stations (56.6°) of 16.6°, while the differences between the 24-hour averages is 14.1°. For the second series, the differences were 15.5 and 14° respectively. The night averages for the two stations naturally show less difference than the 24-hour averages, viz, 11.7° and 12.3°, for the respective periods. Thus, the temperature for the season varies inversely with the altitude of the stations, being highest at the plains, especially during the day, and lowest at the subalpine station, particularly at night. The plains station showed the greatest difference between day and night temperatures and the subalpine the least.

Holard and Humidity.

In total rainfall for the season of 1920 the plains station was lowest with 8.13 inches, the montane second with 10.74 inches, the subalpine highest with 12.13 inches. From the weekly rainfall at the three stations (fig. 7), it will be seen that the last part of the summer received more rain than the first, the maximum at all stations being reached during the week of August 16. It is also evident that, while the average at the subalpine station exceeded that at the montane, the rainfall at the latter was often greater. The rain-gages were kept in close proximity to the phytometers and read weekly, an oil seal being used to reduce evaporation. The holard exhibited no constant difference between the stations, though in general the surface layers of the soil at the plains and the montane stations gave higher readings than at the subalpine, while the deeper layers at the latter were in general moister.

In average relative humidity, the subalpine station was high, the plains second, and the montane low, the averages for the season being 62.5, 62.3, and 59.3 per cent, respectively. The daily 24-hour averages are graphed in figure 7, which shows plainly the general rise of humidity during the latter part of the summer. This same relation of the humidity is shown by comparing the 24-hour average for the period of the first and second series. These averages are 57.7 and 66.9 per cent for the plains station, 55.3 and 63.3 for the montane, and 60.4 and 70.6 per cent for the subalpine station in the first and second series respectively.

In comparing the stations on the basis of the day and the night humidities, the order is changed, the average day humidities for the season being plains 49.4 per cent, montane 51.9 per cent, and subalpine 64.5 per cent, while the corresponding average night values are 77, 68.6 and 71.6 per cent The plains station thus shows the lowest day humidity but the highest night average. This may be expressed in the form of the difference

between the night and day values and gives 27.6 per cent for the plains, 16.7 per cent for the montane, and 7.1 per cent for subalpine station. This variation between night and day humidity was somewhat less during the second series at the plains and montane stations, but greater at the subalpine station, the differences for the plains station being 30.2 and 25 per cent, montane 18.8 and 14.5 per cent, and subalpine station 3.3 and 10.9 per cent for the first and second series respectively. Thus, the average relative humidity for the 24 hours of the day is slightly the highest at the subalpine, second at the plains, and lowest at the montane station, the daily variation being greatest at the plains and least at the subalpine station. The night humidity averages highest at the plains and lowest at the montane station, but the subalpine station yielded the highest day humidity and the plains station the lowest.

Evaporation.

In general, evaporation was highest at the plains, second at the montane, and lowest at subalpine station, the weekly averages for the season being respectively 25.8 c. c., 19.0 c. c. and 17.2 c. c. During most of the season the evaporation at the plains station was markedly above that of either of the others (fig. 7), while for the latter part of the summer, corresponding in time to the second series, the results are lower than for the first series. This reduction in evaporation during the latter part of the season is also shown by comparing the averages for the first series with those of the second series, the values being plains 28.5 c. c. and 23.5 c. c., montane 21.7 c. c. and 14.5 c. c., and subalpine station 21.4 c. c. and 13.3 c. c. The atmometers used were run in duplicate within the screen inclosure of each station, the evaporating surface being set at approximately the level of the leaves of the phytometer plants. The values recorded were averages from the standardized readings of the two instruments.

Wind.

The average weekly wind movement was greatest at the plains, second at the subalpine, and least at the montane station, the values being respectively 366.7, 215.1, and 204.7 miles. The weekly average for the first series is greater at the plains and subalpine stations, but less at the montane station than for the second series. The graph of the weekly totals shows the comparatively high and variable values at the plains station (fig. 7). While the wind at the subalpine was above that at the montane station during the earlier part of the season, it dropped slightly below the latter through most of the late summer period. The anemometers in all cases were located within the screen inclosures on a level approximating that of the leaves.

Summary.

For the period observed, the plains station showed the highest and most fluctuating temperatures, especially during the day, the lowest rainfall, a moderately high surface holard, the lowest relative humidity during the day, but the highest during the night, the greatest total amount of wind, and the highest average evaporation. The subalpine station showed the

lowest and most constant temperature, the greatest rainfall, a relatively low holard in the surface layers but high in the subsoil, the highest and most constant average relative humidity, an evaporation which at times exceeded and at times fell below that at the montane station, and a total number of miles of wind, which, for the season, slightly exceeded that at the montane station, but was little over one-half that at the plains station. The montane station was, in general, intermediate, but on the whole approached conditions at the subalpine more closely than those at the plains station.

The second series of phytometers was operated under conditions of temperature similar to those of the first series, except at the subalpine station, where the early approach of autumn reduced the average somewhat, but under conditions of greater humidity, much greater rainfall, less wind, except at the montane station, and less evaporation.

By a comparison of the physical factors for 1919 and 1920, it is evident that the 1920 phytometers were grown under conditions of lower temperature, greater rainfall, higher holard, greater relative humidity, and less evaporation.

Phytometers, First Series.

Each battery consisted of 5 sealed and 5 unsealed phytometers of each species, 1 plant being used in each sunflower phytometer and 5 plants in each wheat or oats phytometer. The sunflower seeds were soaked and planted June 5 and those of the grains June 6. When the plants were well started, they were transferred to containers filled with soil taken from the same spot as in the previous series. The containers were the same as those used in the second series of 1919 and were filled and sealed in the same way, i. e., by the method of the wax-cloth seal. All phytometers were started at the plains station June 11, at the montane station June 13, and at the subalpine station June 12. They were weighed at all stations June 14 and this weight was taken as initial.

At the time of weighing and watering each week, three measurements were made of each sunflower, viz, the height of stem, stem diameter 1 cm. above the surface of the seal, and the extreme length and width of each cotyledon or leaf-blade. For the grains, the measurements consisted merely of the extreme width and length of each blade, measurements of length being taken from the ligule, and the number of stems per container. To get as accurate an estimate as possible of the weekly leaf-area from these measurements, about 300 sunflower leaves of various sizes and taken from various parts of plants grown from the same lot of seed as that used for the phytometers were measured under conditions similar to those in the experimental areas. They were then removed from the plant and blueprints made, the areas of the latter being obtained later by duplicate readings with a planimeter. The leaf-areas in square centimeters thus obtained were compared with the product of the leaf dimensions measured in millimeters and the average factor found that would give the area of both sides of the leaf from the product of its dimensions. This method was applied to sunflower leaves and cotyledons as well as to the leaves of the grains. For the sunflower leaves it was found that the area of both sides of the leaf

in square centimeters is obtained by dividing the product of the leaf dimensions in millimeters by 79, thus giving a factor of approximately 0.013. In practice, the area of the sunflower leaves in square centimeters was found from the product of the extreme dimensions in millimeters, by multiplying by 0.013. Results obtained by a similar method gave for sunflower cotyledons the factor 0.016 and for grain leaves 0.015. To make sure of the applicability of this factor to leaves grown in the field, it was

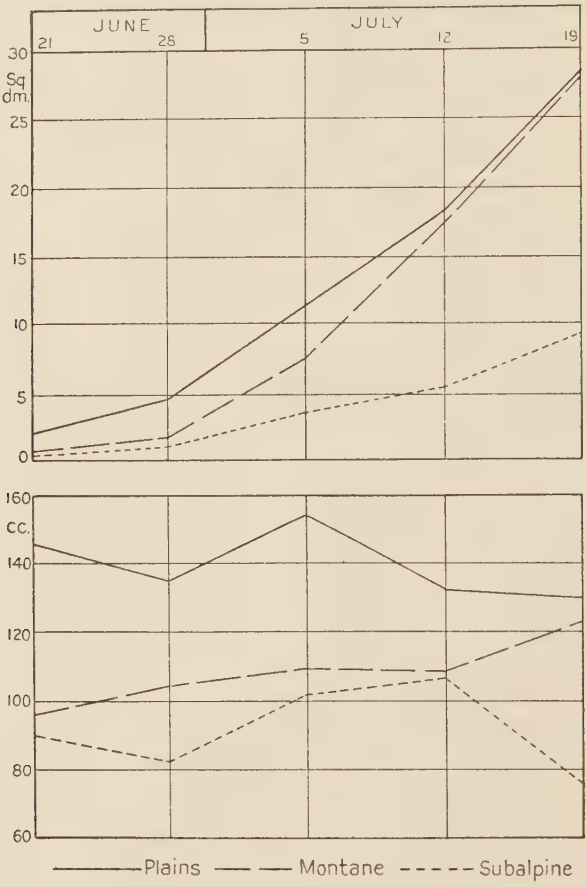


FIG. 8.—Average leaf-area and transpiration of sunflowers, first series, 1920.

carefully checked against leaf-areas obtained by the planimeter from blueprints made from the leaves of field-grown plants. In case a part of the leaf was lost through accident, the area of the destroyed portion was carefully estimated and subtracted from the area of the leaf as computed by the above method. All leaves which appeared withered were removed and filed in envelopes under the number of the phytometer from which they came, so that the entire dry weight could be found at the end of the series.

On July 19 all plants were cut at the surface of the seal after the above measurements had been made, and the green weight of the plant-tops grown

in each phytometer was obtained. The plants were then brought to the laboratory and a few of the leaves removed and blue-prints made, in order to check the factor used in obtaining the area against any possible variation in leaf-shape due to the peculiar conditions at the various stations. The plant material taken from each phytometer was cut into small pieces, dried in an oven, cooled in a desiccator, and weighed.

TRANSPIRATION.

The transpiration per unit leaf-area varied in general inversely with the altitude, being greatest at the plains and least at the subalpine station. In weekly water-loss per square decimeter of leaf-area (fig. 8), there is a rather close correlation between the curves for the plains and for the subalpine sunflowers, the transpiration for the week of July 12 being the only

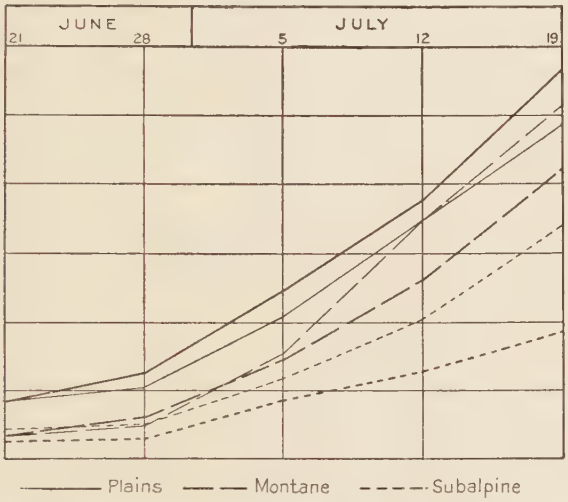


FIG. 9.—Average stem-length (heavy lines) and diameter (light lines) of sunflowers, first series, 1920.

one for which the rates do not agree. On the other hand (figs. 10 and 11), there is a better correlation between the transpiration of wheat and oats at the montane and subalpine stations than between the plains and either of the others. The great decline in the transpiration-rate of plains wheat and oats during the third week of the series is surprising, since it coincided with an increase in average daily evaporation and total weekly wind, but harmonizes with the beginning of a decline in the rate of leaf-growth for these two plants, though not for the sunflowers growing under the same conditions. Evidently, the conditions which became operative at the plains station the week ending July 5 caused a slight reduction in the rate of leaf-growth and in the transpiration per unit leaf-area of wheat and oats, but permitted a slight increase in the transpiration of the sunflowers and had no noticeable effect on the rate of leaf expansion. At the same time that the grains at the plains station fell from a high to a low rate, the plants at the montane and subalpine stations agreed in starting from a low rate of water-loss and rising to a comparatively high one. Since there was an

increase in rainfall at all the stations, and since the sunflowers were not affected, it seems that the factors operative in reducing the leaf-growth and water-loss for the plains wheat and oats were physiological rather than physical.

To facilitate comparison between the average transpiration per unit leaf-area for the various plants and the factor readings, the transpiration curves have been plotted, together with those of average temperature, average relative humidity, average daily evaporation, and total weekly wind (figs. 12, 13, 14). In figure 12 the sunflower transpiration curve is roughly the reciprocal of all the instrumental curves and is a particularly good reciprocal of those for relative humidity and evaporation. At the plains station

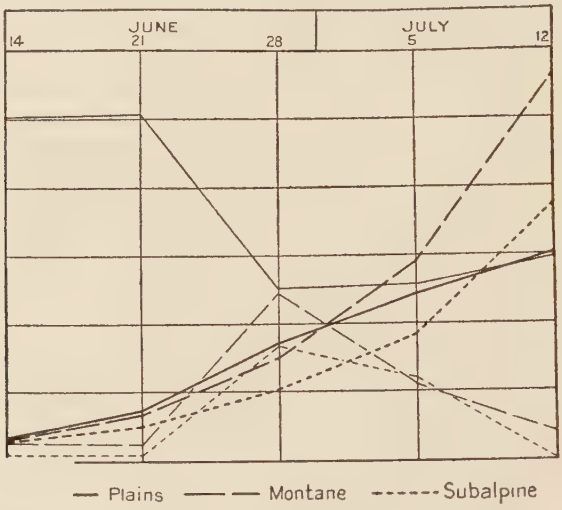


FIG. 10.—Average leaf-area (heavy lines) and transpiration (light lines) of wheat, first series, 1920.

the transpiration of the sunflowers was apparently affected by factors other than those in control of evaporation from the atmometer cups. At the montane station, however, the transpiration curve, while the reciprocal of the humidity curve as for the plains station, shows close correlation with the temperature curve and also with the curve of average evaporation. Evidently in this case temperature and evaporation are good indexes of the transpiration of these leaves, and probably temperature was the controlling factor for both transpiration and evaporation. In the curves from the subalpine station, while there is no close correlation, there is a general one with evaporation, temperature, and relative humidity. Thus, transpiration per unit leaf-area in the sunflowers regularly gives a correlation with average temperature, average relative humidity, average evaporation, and total wind, though the behavior at the plains station was more or less exceptional.

The transpiration of the plains wheat (fig. 13) is not correlated closely with any instrumental curve, but shows the best relation to the curve of average relative humidity. There is a general correlation with all the

instrumental curves, but the transpiration of the plains wheat varied in a manner the reverse of that of the sunflowers under the same conditions. The transpiration of the montane wheat shows a positive correlation with the curves of average temperature and average relative humidity. The subalpine curves are compared in figure 13. This shows again, as in figure 12 for the sunflowers, a negative correlation of the transpiration with average relative humidity and a positive correlation between the transpiration and the average temperature and evaporation curves. The transpiration of wheat varied in general with average temperature, average relative humidity, average evaporation, and total wind at the plains station, with average temperature and evaporation and inversely with average

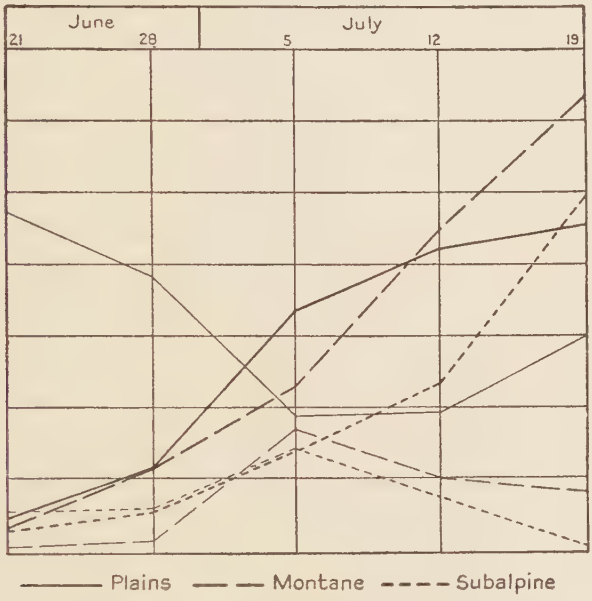


FIG. 11.—Average leaf-area (heavy lines) and transpiration (light lines) of oats, first series, 1920.

relative humidity at the montane station, and with average temperature and evaporation and inversely with average relative humidity at the subalpine station.

There is a general correlation of the transpiration of the plains oats with average temperature, average evaporation, average relative humidity, and total wind (fig. 14). Assuming that the transpiration results for the first week might have been abnormal because of the recent transplanting and sealing of the plants, the closest correlation is with the curve of average temperature. The transpiration of oats in the montane zone shows a rather close correlation with average temperature, evaporation, and average relative humidity. The same relation is, in general, true for the results from oats at the subalpine station. The transpiration per unit leaf-area of the oats varied directly at all the stations, as did the wheat, with average temperature and evaporation, and inversely with the average relative

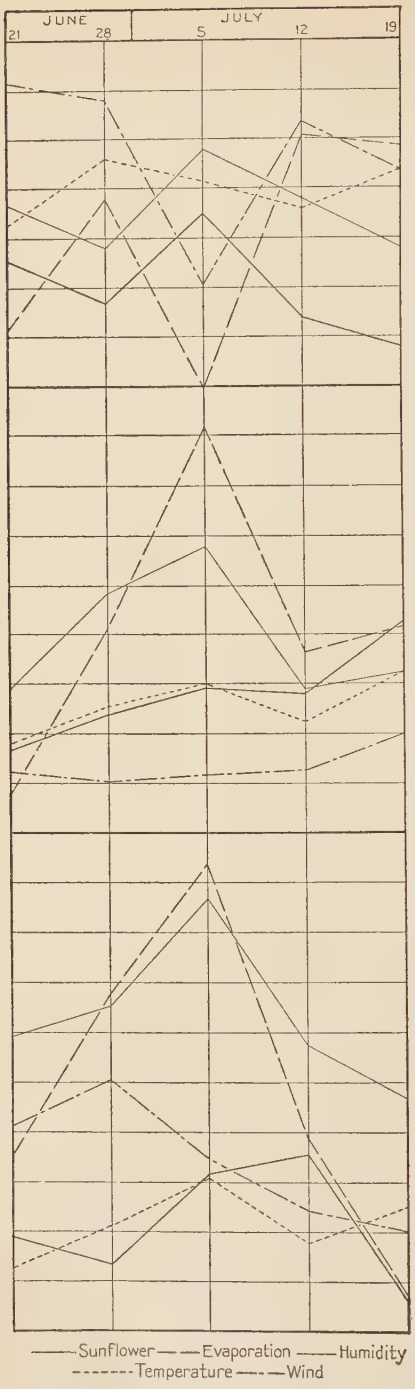


FIG. 12.—Average transpiration of sunflowers and physical factors, first series 1920 (humidity curves inverted): plains (below), montane (middle), subalpine (above).

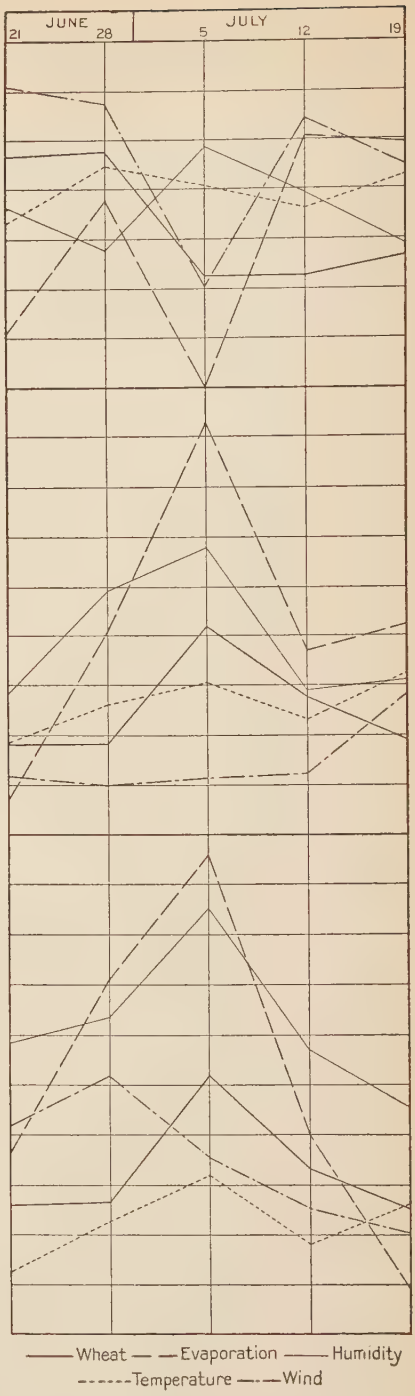


FIG. 13.—Average transpiration of wheat, and physical factors, first series, 1920 (humidity curves inverted): plains (below), montane (middle), subalpine (above).

humidity at the montane and subalpine stations. The frequent discrepancies in the agreement of the curves indicate the importance of physiological as well as physical conditions.

Growth.

The weekly increase in leaf-area of the sunflowers was highest at the plains, second at the montane, and lowest at the subalpine station (fig. 8). The leaf-area began high at the plains station because the plants were first installed there and hence recovered from the shock of transplanting before those at the upper stations, but the increased rate of growth of the montane plants brought the leaf-area to a point approximately equal to that of the plains phytometers. In contrast to this, the subalpine sunflowers maintained a comparatively slow rate of growth and showed little acceleration during the time of this series. As to leaf-area of wheat and oats (figs. 10 and 11), the relation of the stations is markedly different. Both showed a similar initial rate of leaf-expansion at all stations, but after the third week of the series the rate of growth at the plains station fell off so rapidly that by the end of the experiment the leaf-area at the plains station was exceeded by that at both the montane and subalpine stations. Beginning with the week of June 28 to July 5, there was a marked increase in evaporation at the plains station over that at the other stations, a fact perhaps explained by the simultaneous rise in wind, since there was little change in average temperature and an actual increase in rainfall and average relative humidity. The behavior of the cereals at the subalpine station was also strikingly different from that of the sunflowers. Instead of maintaining a more or less constant rate of growth to the end of the series, wheat and oats agree in showing a great acceleration in rate of leaf-expansion throughout the period of the experiment.

Increase in stem-length for the sunflower followed the leaf-growth closely (fig. 9). After the first two weeks, during which recovery from transplanting took place most rapidly at the plains station, and least so at the subalpine, the rate of stem-elongation continued about the same at the plains and montane stations throughout the series, but was much less at the subalpine one. Unlike the rate of leaf-growth, the rate of stem-elongation at the montane did not exceed the rate at the plains station. However, the rate of increase in the diameter of the stems at the plains was never equal after the second week to that at the montane station and in fact barely exceeded that at the subalpine one. All stem diameters were measured by means of a vernier caliper reading in millimeters and tenths, while the stem-length was taken by a ruler, the measurement being the distance from the surface of the seal to the base of the terminal bud.

Dry Weight.

With respect to green and dry weights, plants at the plains station gave the highest figures, those of the montane next, and those at subalpine lowest. This is in agreement with the leaf-area of the sunflowers, but not with the size of the cereals as indicated by their leaf-area (figs. 10 and 11). Thus, the wheat and oats showed a final leaf-area greater at the montane

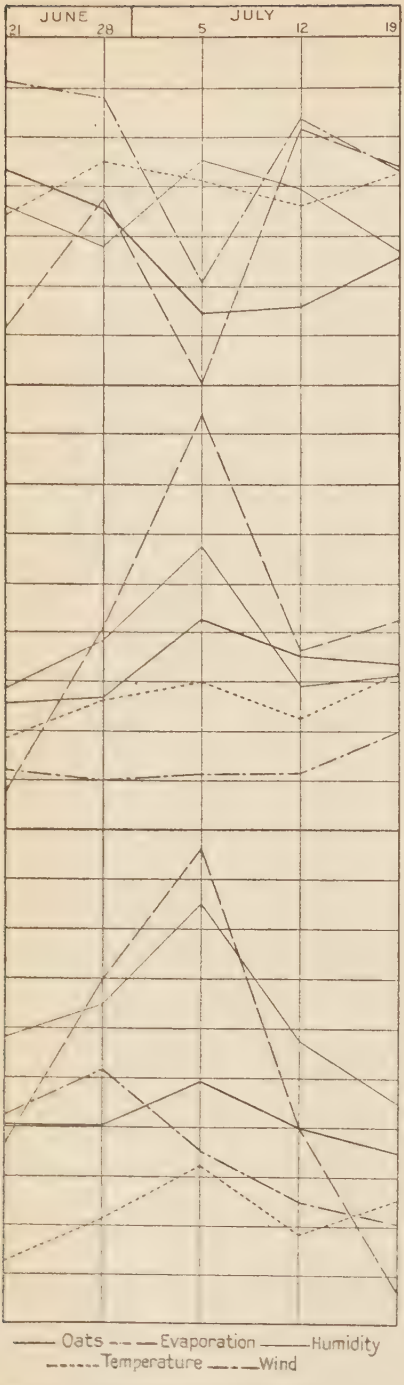


FIG. 14.—Average transpiration of oats, and physical factors (humidity curves inverted): plains (below), montane (middle), subalpine (above).

and subalpine stations than at the plains station, but a greater dry weight at the latter than at either of the upper locations. This difference in the growth of the plants at the various elevations is shown more clearly by the percentage relation between green weight and dry weight. This percentage decreases with the increasing altitude of the stations at which the phytometer plants were grown. Expressed in other words, the plants showed increasing succulence with the increasing altitude of the stations where

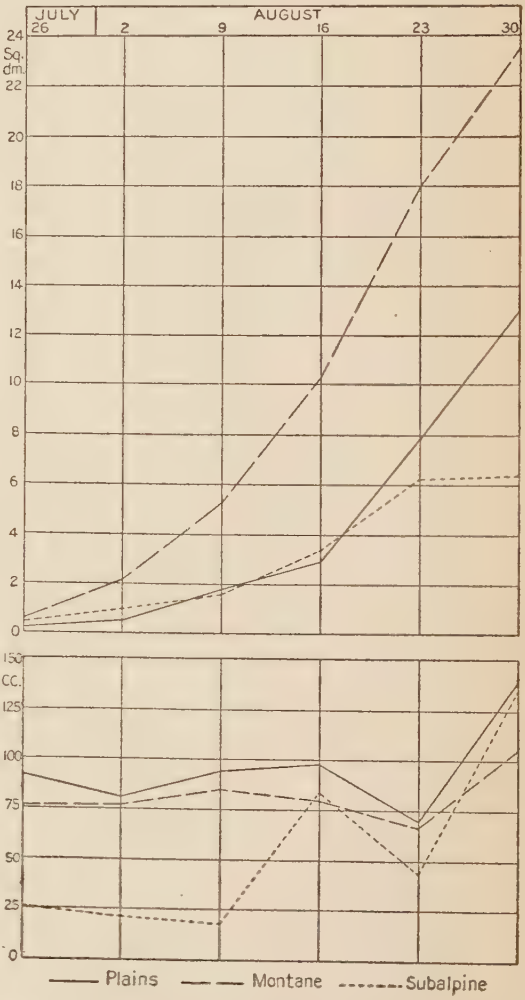


FIG. 15.—Average leaf-area and transpiration of sunflowers, second series, 1920.

they developed. The data for unsealed check phytometers shows that, measured by either green or dry weight, these were not consistently larger than the sealed phytometers. The percentages correspond in general with those already given for the sealed plants.

Water Requirement.

The water requirements of the plants in this series are similar to those obtained in the earlier part of this work in that they were greatest at the plains station. They differ from preceding results in being more nearly equal for all the stations, and also in the fact that sunflower and wheat gave values at the montane station lower than those for the subalpine. The water requirements for sunflowers were 456.3, 415.07, and 434.29, for wheat 650.99, 530.7, and 543.35, and for oats 543.35, 532.41, and 520.96 at the plains, montane, and subalpine stations respectively (fig. 24). These values are in general below those obtained for the plants of the second series of 1919, and this is likewise true when the comparison is made with the sunflowers of the first series of 1919.

Summary.

On the whole, transpiration per unit leaf-area was greatest at the plains station, less at the montane, and least at the subalpine for all species. The transpiration rates of the grains were in fairly close agreement, but differed materially from that of the sunflower. The transpiration of the sunflowers showed no positive correlation with any instrumental curve at the plains station, but was correlated negatively, in a general way, with all. At the montane and subalpine stations, however, the sunflower transpiration correlated positively with the average temperature and evaporation curves and negatively with the curve of average relative humidity. The transpiration of wheat and oats showed a general positive correlation with all instrumental curves at the plains station and with average temperature and evaporation at the montane and subalpine stations and a negative correlation with average relative humidity at the montane and subalpine stations. As a criterion of transpiration, evaporation as measured by the white cylindrical atmometers showed no greater correlation than other factors, such as temperature.

For sunflower, the smallest growth occurred at the subalpine station in leaf-area, stem-length, and stem-diameter. The greatest stem elongation took place on the plains, but the greatest increase in stem-diameter in the montane zone. The initial rate of leaf-expansion for the sunflower was greatest at the plains station, but was exceeded by the rate at the montane station during the latter half of the series, the sunflowers finally showing the greatest leaf-area and stem-length on the plains, but the greatest diameter at the montane station.

Wheat and oats agreed in showing the most rapid leaf-expansion on the plains for the first part of the series, but a marked decrease in the growth-rate occurred after the third week, so that the final leaf-area of the cereals was less at the plains station than at the others.

In size, as measured by both dry and green weight, the three species were largest at the plains, second at the montane, and smallest at the subalpine

station. In view of the fact that the final leaf-area of the plains and montane sunflowers was approximately equal and of the wheat and oats was greater at the montane than at the plains, it is evident that the montane plants had more leaf-surface in proportion to their mass than the plants on the plains.

The percentage relation of dry weight to green weight decreased with the increasing altitude of the stations at which the plants were grown.

No marked dwarfing effects due to sealing were evident.

The water requirement, while slightly largest at the plains station for all three species, was on the whole not less at the subalpine than at the montane station. For sunflower and oats the difference was so small as to be within the limits of error, but wheat gave a value materially higher for the plains station.

During the first series the sunflowers at the plains station attained greater height, slightly greater leaf-area, and greater dry and green weight with less proportional water in the tissue than at any other station, but were second to the montane sunflowers in stem-diameter. The water requirements of sunflower and oats were hardly greater at the plains than at the other stations, but the value for wheat at the former was considerably above that at the other two stations. All the plants showed a greater succulence when grown at increased altitudes, and likewise agreed in producing more leaf-surface in proportion to their green and dry weight at the montane than at the other stations.

Second Series.

For the second series the same methods were employed as for the first, the kinds and numbers of plants, stations, containers, and soil being identical. The sunflower achenes were soaked and planted in flats July 14; they were transplanted to the containers and sealed at the various stations on July 21 to 23. The seeds of the cereals were soaked and placed in germinators July 19 and planted in the containers on the same dates. These containers were not immediately sealed and weighed, however, as the wheat and oats seedlings made poor initial growth. The holard found in the containers was: plains 15.25, montane 14.8, and subalpine station 16.9 per cent. The plants were removed August 30, bringing the series to a close. The only obvious difference from the first series was the poor growth of the wheat at the plains station, making replanting necessary the second week of the series.

Transpiration.

In general, the transpiration per unit leaf-area, as in the first series, varied inversely with the altitude of the stations. The transpiration curves for the sunflowers at the various stations, unlike those of the first series, exhibit a fairly close correlation (fig. 15). However, wheat at the plains station gave a low transpiration-rate, falling below the montane station for all but the final week of the series (fig. 17), but this is not surprising in view of its poor growth. The curves of transpiration for montane and subalpine wheat are closely correlated, neither showing much increase until

the final week of the series. The transpiration of oats (fig. 18), while giving rather poor correlation between the stations, agrees rather closely with the sunflower values at the montane station, but not elsewhere.

The transpiration of the plains sunflowers shows no close positive correlation with any instrumental curve. There is a negative correlation with the curve of average relative humidity (fig. 19), but the average temperature is quite as good a measure of transpiration as evaporation, neither

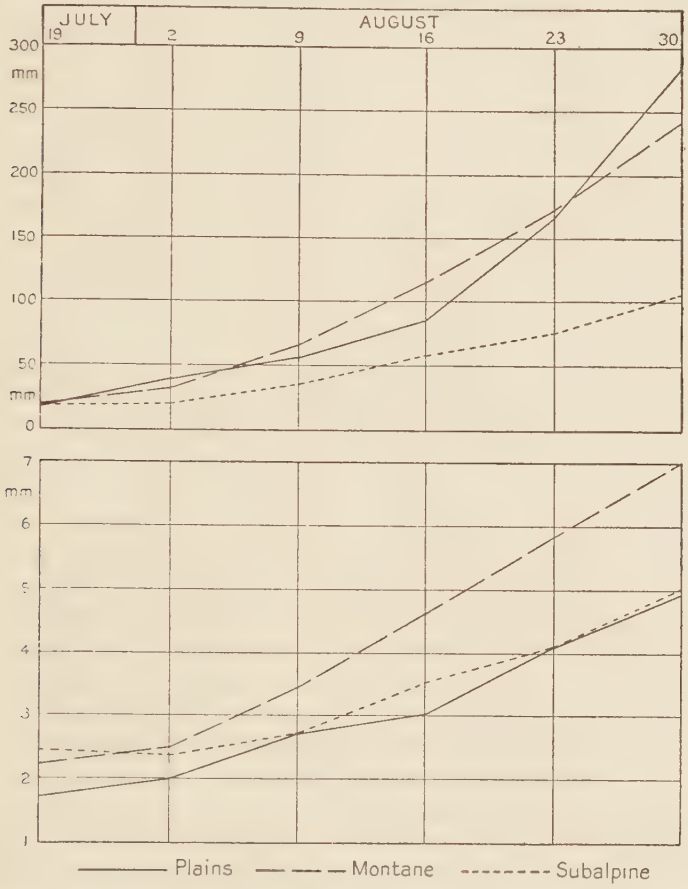


FIG. 16.—Average stem length and diameter of sunflowers, second series, 1920.

agreeing with the transpiration curve. The transpiration of the montane sunflowers shows much the same result as the above (fig. 19), there being a poor negative correlation of the transpiration curve with that of relative humidity and an equally poor positive correlation with the temperature and evaporation curves. The transpiration of the subalpine sunflowers gives an even poorer correlation with the physical factors for that station. There is a negative correlation with the relative humidity curve and a rough positive correlation with the curves of temperature and evaporation. The transpiration of the sunflowers showed a negative correlation with the

average relative humidity, but no close positive correlation with any instrumental readings made.

Plains wheat exhibits a fairly close positive correlation between transpiration, temperature, and wind, but no correlation between the transpiration curve and that of evaporation or humidity (fig. 20). Montane wheat gives a positive correlation between transpiration, evaporation, and temperature, but no consistent variation with wind or relative humidity. At the subalpine station the relations are similar in that there is no close correlation between the curve of transpiration and that of any of the instrumental results.

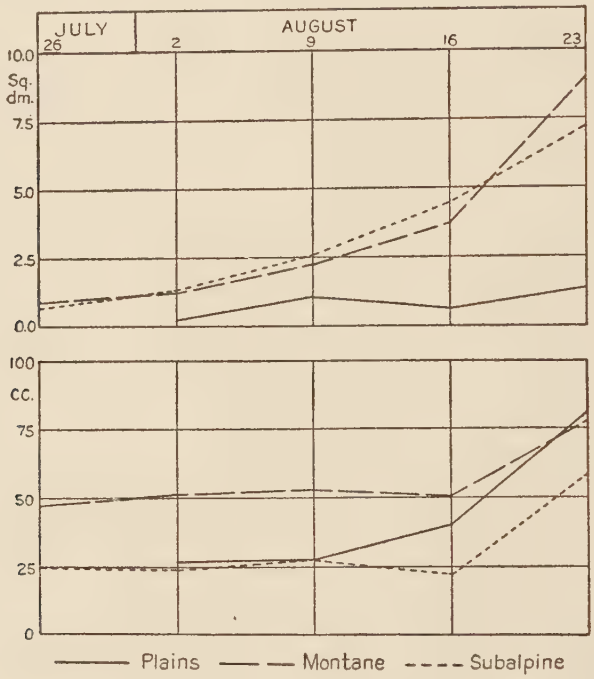


FIG. 17.—Average leaf-area and transpiration of wheat, second series, 1920.

The transpiration of the plains oats shows a close positive correlation with the evaporation and a fair negative correlation with average relative humidity (fig. 21). At the montane station the transpiration curve also exhibits a general agreement with the curve of average evaporation and a rough negative correlation with the relative humidity curve. The results for the subalpine oats show a close positive correlation between the wind and the transpiration, as well as a general positive correlation between the transpiration and evaporation curves.

The transpiration values for the second series thus show that roughly the sunflowers varied at the plains station directly with evaporation and inversely with relative humidity, at the montane station directly with evaporation and temperature and inversely with relative humidity, and

at subalpine station directly with evaporation, temperature, and wind and inversely with relative humidity. Wheat at the plains station agreed directly with evaporation, temperature, and wind, at the montane station directly with evaporation, and at the subalpine station directly with temperature. Oats varied at the plains and montane stations directly with

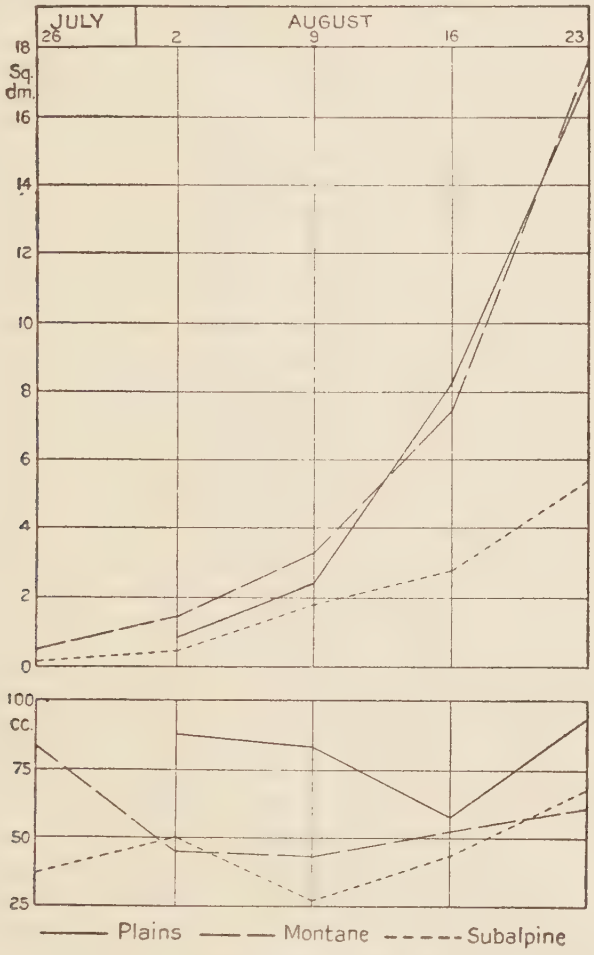


FIG. 18.—Average leaf-area and transpiration of oats, second series, 1920.

evaporation and inversely with relative humidity, and at the subalpine one directly with wind and evaporation. The correlations were more or less imperfect in nearly all cases.

GROWTH.

The weekly leaf-areas were highest at the plains station in every case. Leaf-growth at the montane station was greatest from the beginning, but the rate at the plains and subalpine stations did not vary greatly until after the fourth week, the greatest difference occurring the last week.

Thus, on August 23 the area of the subalpine sunflowers was 6.17 sq. dm. and on August 30, 6.26 sq. dm., while the area of the plains sunflowers was 7.8 and 12.83 sq. dm. respectively. On the same dates the montane sun-

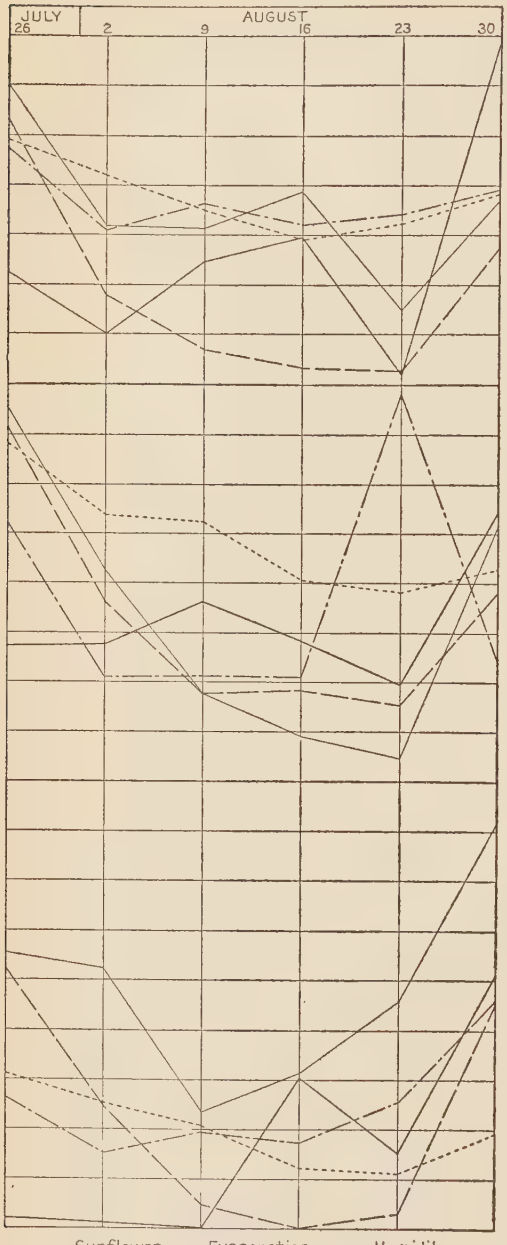


FIG. 19.—Average transpiration of sunflowers, and physical factors, second series, 1920 (humidity curves inverted): plains (below), montane (middle), subalpine (above).

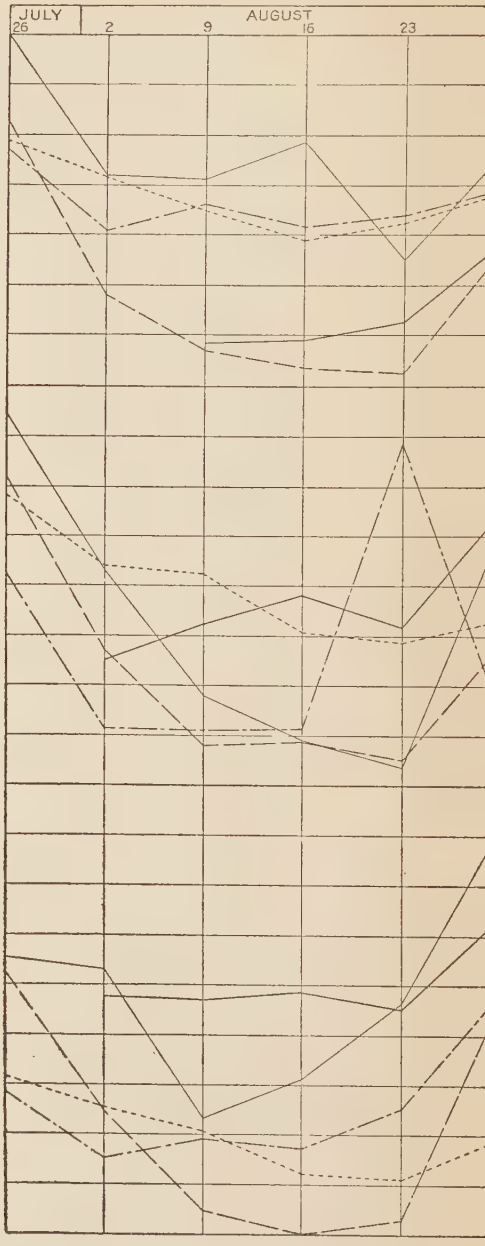


FIG. 20.—Average transpiration of wheat, and physical factors, second series, 1920 (humidity curves inverted): plains (below), montane (middle), subalpine (above).

flowers yielded areas of 17.91 and 23.51 sq. dm., or about twice that of the plains plants (fig. 15). The leaf-area of the wheat was very low for the plains station (fig. 17), the plants at the montane and subalpine stations being very much larger. This is explained by the fact that the wheat seedlings on the plains did not recover from transplanting and were replaced the second week of the series. The phytometers at the montane and plains stations gave similar weekly increases, the rate of leaf-expansion diverging markedly only during the last week, when the rate of the montane plants exceeded that for the subalpine station. The oats gave a rate of leaf-growth more like that of the sunflower than of the wheat (fig. 18). As in the sunflowers, the final area of the montane oats was greatest, but the plains oats, in spite of their late start, soon attained approximately the same leaf-area as those at the montane station and maintained a similar rate to the end. The subalpine oats showed a low rate of growth and a small leaf-area throughout the series.

As to leaf-area, the montane station yielded in general the highest values for all plants. The plains oats, however, gave an area approximately equal to that of the montane plants. The plains sunflowers, while somewhat larger than the subalpine ones, were far smaller than the montane. The plains wheat had the smallest leaf-area of the series, while the subalpine station exhibited the lowest leaf-area for oats and sunflowers, but produced wheat with a leaf-area almost equal to that of the montane plants. In average stem elongation the sunflowers at the plains and montane stations gave similar values (fig. 16), the main difference being the increased rate of the former during the final week of the series, an increase which raised the average considerably above that for the montane group. In stem-length the subalpine sunflowers were far below those at the other stations while the stem-diameter was greatest at the montane station. The plains-station values remained low, never even exceeding those from the subalpine station plants. The subalpine sunflowers were small both as to stem-length and diameter, while montane sunflowers were largest in both stem-length and diameter during the first part of this series, but were exceeded in stem-length by the plains sunflowers during the last week of the experiment.

Dry Weight and Water Requirement.

As measured by the green weight of the tops, the sunflowers and wheat made the best growth at the montane station, but the oats made a slightly better growth at the plains than at the other stations. The percentage relation between dry weight and green weight shows that the sunflowers display the same relation as that already discussed for the preceding series, viz, the percentage decreases with the increasing altitude of the stations at which the plants were grown. For the cereals, on the other hand, the relation is reversed, i. e., the percentage increases with increasing altitude. For the wheat this is not so surprising when one recalls that the plains plants made such poor growth as to necessitate replanting and hence were younger and more succulent than the plants at the other stations. The size of the plants as indicated by the dry weights corresponds to the relation discussed under leaf-area, viz, the sunflowers and wheat were largest at the

montane station, the sunflowers smallest at the subalpine station, and the wheat smallest at the plains station. The oats showed the greatest dry weight at the plains station, second at the montane station, and smallest at the subalpine station. No conspicuous dwarfing effects due to sealing were evident from a comparison of the green and dry weights of the sealed and unsealed phytometers.

The water requirement (fig. 24) of sunflower was similar to that obtained in the first series, the plains station being highest with a value of 437.1, the montane lowest with a value of 357.04, and the subalpine intermediate with that of 396.6. For wheat and oats, however, water requirement was greatest at the plains station in every case, and least at the subalpine, thus decreasing with increasing altitude, as in the series for 1918 and 1919.

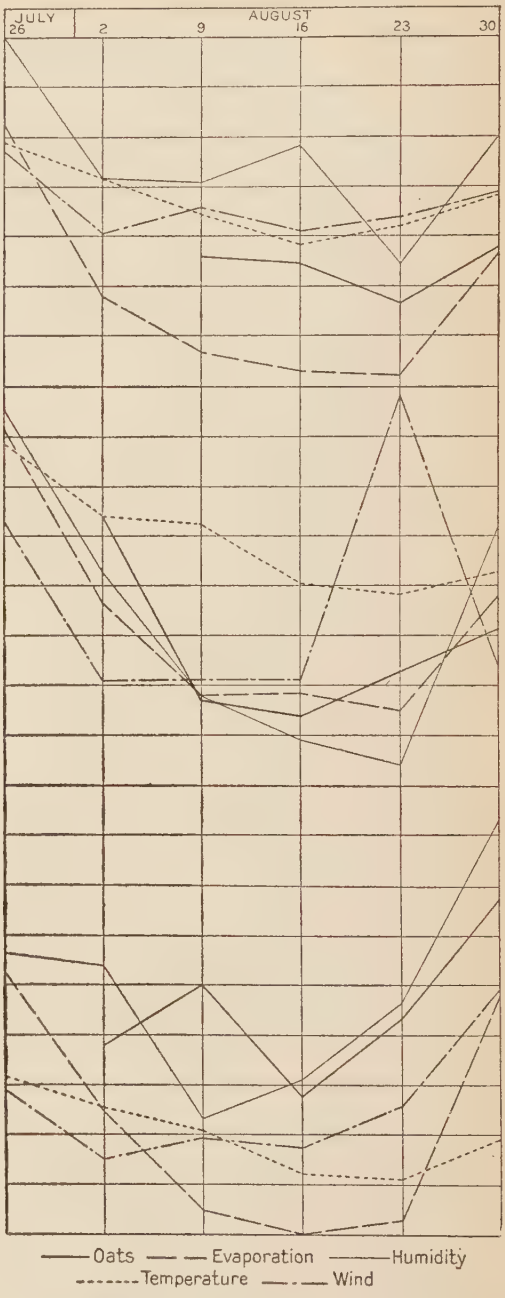


FIG. 21.—Average transpiration of oats, and physical factors, second series, 1920 (humidity curves inverted): plains (below), montane (middle), subalpine (above).

SUMMARY.

The transpiration per square decimeter of leaf-area decreased from the plains through the montane to the subalpine climax as in the first series. The plains wheat, however, gave a value below that of the montane station. There was no close agreement between the transpiration of wheat and oats, contrary to the results in the first series. At the plains station the transpiration of sunflowers varied directly with evaporation and inversely with relative humidity, while at the other two stations it varied directly with temperature also. The transpiration of wheat fluctuated directly with temperature and wind at the plains station, with evaporation and temperature at the montane station, and with temperature at subalpine

station, and that of oats varied directly with evaporation and inversely with relative humidity at the plains and montane stations and directly with evaporation and wind at the subalpine. The evaporation from standardized, white, cylindrical atmometer cups gave no better indication of the water-loss from plants than other factors, such as average temperature.

The sunflowers made the best growth in leaf-area and stem-diameter at the montane, but the greatest growth in stem-length at the plains station. Growth as measured by leaf-area, stem-length, and stem-diameter was least at the subalpine station, but the difference in leaf-area and stem-diameter between this and the plains was small. Wheat in general showed the greatest leaf-area at the montane station, with the subalpine a close second. The leaf-area of the oats was high at the montane and plains stations and low at the subalpine one.

As measured by both dry and green weight, the sunflowers were largest at the montane, second at the plains, and third at the subalpine station; the wheat largest at the montane, second at the subalpine, and smallest at the plains station; and oats largest at the montane, second at the plains, and smallest at the subalpine station. Since the final leaf-area of the oats was slightly greater at the montane than at the plains station, and the dry and green weights showed the reverse relation, the oats plainly agree with those of the first series in showing a greater leaf-area in proportion to their weight at the montane than at the plains station. The other plants, however, do not show this relation. The percentage relation of dry weight to green weight decreases with the increasing altitude of the stations for the sunflowers, although the unsealed checks show a slightly greater value for the subalpine than for the montane station. Relations for the wheat and oats are, in general, the reverse of this, although the wheat checks show little difference between the stations and the oats have the highest value at the montane station.

The water requirement, as defined by Briggs and Shantz, was greatest in every case at the plains station; it was least at the montane station for sunflowers, but at the subalpine for wheat and oats, in accordance with their boreal character.

During the second series the sunflowers grew to a greater height at the plains station, but gave a greater stem-diameter, leaf-area, and green and dry weight at the montane station. The water requirement was greatest at the plains station, decreasing with increasing altitude for wheat and oats, but was smallest at the montane station for the sunflowers. The values for the leaf-area proportional to the weight and for the succulence of the plants vary in the different cases.

Large Phytometers.

Since large containers are difficult to handle as well as expensive to install in the mountains, the smaller containers, described in connection with the 1919 series, were used in the greater part of this investigation. While there seemed no good reason to doubt the validity of results obtained from small containers when the results were secured before the roots became crowded, it was thought desirable to use larger containers to check this.

Batteries of sunflower phytometers in galvanized-iron containers, 45 cm. deep by 30 cm. in diameter, were established at the plains and montane stations in 1919, but the accidental destruction of the plants precluded obtaining results of value. In 1920 a battery of three wheat phytometers, two sealed and one unsealed check, was installed at the plains and also at the montane station at the same time and under the same conditions of soil, and with the same methods as those employed for the smaller containers. It was hoped that the results would indicate whether the 6-weeks period was too long for dependable results from the latter. The size of the phytometers necessarily made the method of weighing less accurate than that employed for the small containers. At the time of watering, each container was removed from the soil, wiped dry, and weighed carefully by means of a pair of steelyards weighing to 4 ounces, water being added to restore the original weight, as in the case of the smaller cans (plate 3B).

FIG. 22.—Average transpiration of large phytometers and wheat, first series, 1920.

Wheat was substituted for the sunflowers used in 1919, because the great water-loss from the latter made more frequent watering necessary. However, this choice was unfortunate, as the season at the plains station proved to be unsuited for the good development of wheat. The destruction of some of the plants by grasshoppers was the climax of misfortune at that station and left the data from the montane station as the only trustworthy results available for comparison with those obtained by the use of the small containers. Nevertheless, the lack of complete results from the plains does not greatly impair the value of the data from the montane station for purposes of comparison (fig. 22).

The transpiration per square decimeter of leaf-area for the large phytometers is plotted in figure 22, together with the results from the montane wheat for the first series, this series being used because the plants were handled in identically the same way as those of the large phytometers, except for the differences involved in the size of the container. As the large phytometers were carried through the season, this curve extends to August 30. It will be seen that there is a general decline in the curve with the advance of the season and the age of the plants. Except for the com-

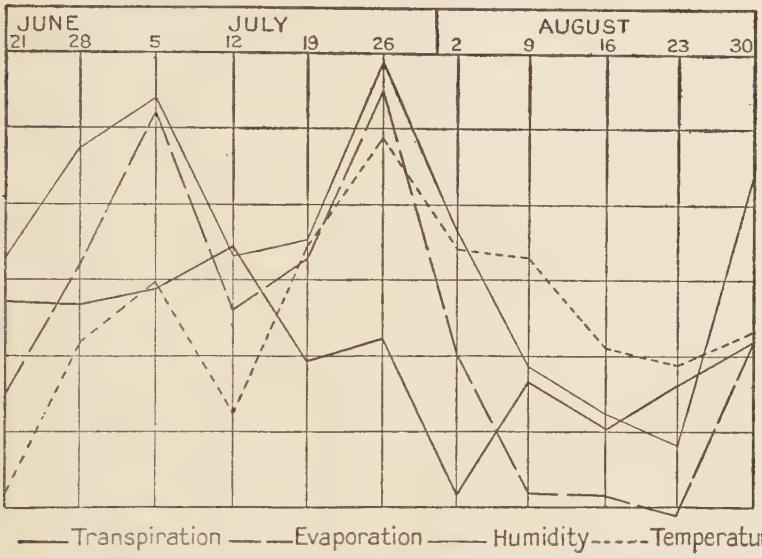


FIG. 23.—Average transpiration of large phytometers, 1920, compared with factor data.

paratively high value for the week, June 28 to July 5, the transpiration rate of the montane wheat corresponds well with that of the wheat in the larger containers, the average transpiration for the five weeks being 84.3 c. c. for the former and 84.2 c. c. for the latter.

A comparison of the weekly leaf-areas shows no indication of abnormal growth for the wheat in the small containers (figs. 10 and 17), and this is essentially true also of the rate of leaf-expansion for the large and small containers.

GENERAL SUMMARY, 1918–1920.

1. The transpiration per square decimeter of leaf-area was highest at the plains, lower at the montane, and lowest at the subalpine station, this relation persisting whether the weekly or the final area was used as a basis. The transpiration did not vary consistently with any single instrumental record. No better correlation obtained between transpiration and evaporation from a white cylindrical atmometer cup than between transpiration and average temperature.

2. The leaf-area, both final and weekly, was usually greatest at the montane and second at the plains station, though the weekly area was

subject to great relative variations. The stem-diameter of sunflowers was greatest at the montane and second at the plains station, but the stem-length was greatest at the plains, the subalpine values for both diameter and height being low.

3. The size of plants as measured by both green and dry weights varies relatively, the largest plants being produced at times at the montane station and at other times at the plains station. In general, however, plants with a high optimum temperature, such as sunflowers, made the best

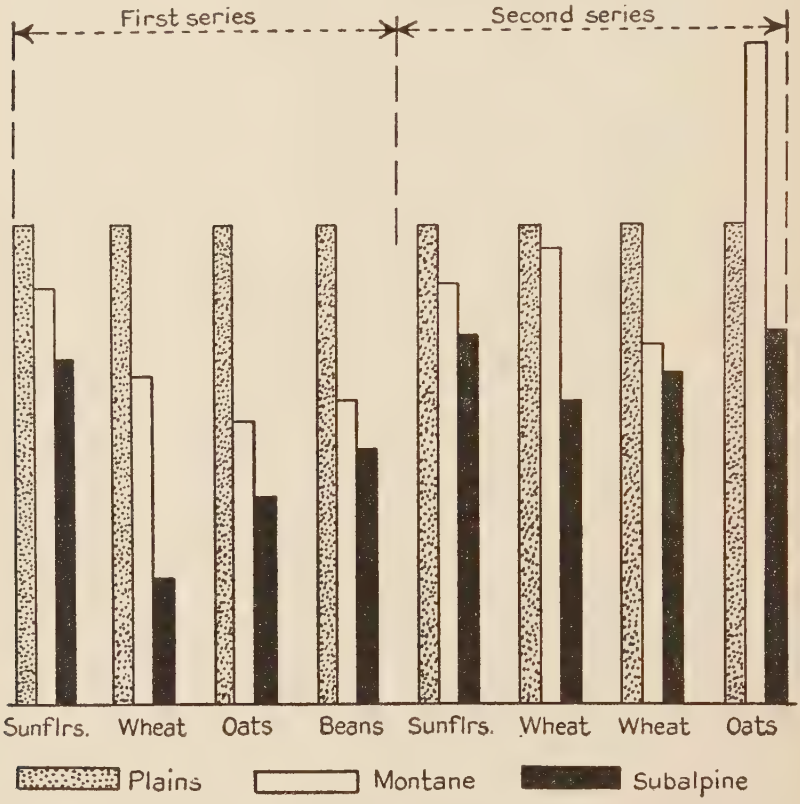


FIG. 24.—Comparative water requirements of plants of first and second series, 1920.

growth at the plains station during the early part of the summer and at the montane station during the late summer, while plants with a lower optimum, such as wheat, made the best growth at the montane station.

4. The water requirement, as defined by Briggs and Shantz, generally decreases with the increase in altitude of the stations at which the plants are grown. This increase in growth efficiency with increasing altitude is variable, however, and under some environmental conditions the relation may be reversed.

5. No harmful effects appeared to result from sealing. The results from phytometers in large containers indicated that no abnormal effects ensued from the use of small containers for the periods concerned.

METHODS AND RESULTS, SEASON OF 1923.

In order to obtain stations in which the control was exerted by a single factor, the selection was made on the basis of light intensity. One station was located in full sunshine, another in half-shade approximately, and the third in dense shade (plates 5, 6A). These were all on essentially the same level and within 100 yards of each other in the narrow valley of Ruxton Brook, which flows past the Alpine Laboratory. They thus afforded the maximum differences in physical factors consistent with accessibility and economy of time and effort, and were in sharp contrast with the stations of preceding years, which were several miles apart and in different climax zones. The sun station was carpeted with grasses, of which *Poa pratensis, Bromus ciliatus, B. pumpellianus,* and *Agropyrum caninum* were the most important. In the half-shade station the cover consisted chiefly of *Thalictrum fendleri, Geranium richardsoni, Zygadenus elegans,* and *Gentiana amarella* beneath a canopy of *Pseudotsuga mucronata.* The light intensity of the full shade was too low to permit the growth of herbs, except for scattered shade forms of two or three species. The instrumental installation at each station consisted of ecographs for recording humidity and the temperature of the air and soil, and of anemometers and atmometers for measuring wind and evaporation respectively. Light intensities were determined by means of stop-watch photometers, and the sums obtained by chemical photometers.

FIRST SERIES.

Sunflower seeds of the ordinary cultivated variety were planted on May 29 and later transplanted from the flats to 3-inch pots rendered impervious by closing the bottom with a paper disk and dipping in melted paraffin. The plants were then moved from Colorado Springs to the Alpine Laboratory and after 2 days for adjustment were sealed by fitting a collar of plastocene modeling clay tightly about the base of the stem and pouring melted paraffin over the surface of the soil. 100 plants were thus sealed, weighed, and the leaf-product determined; they were then exposed at the sun station for standardization. During this period of a week, the individual plants were frequently moved about in the inclosure to eliminate differences arising from location. At the close of the period, the weight and leaf-area were again determined (table 19), and the individuals selected for the respective batteries, plants with too great deviation or otherwise undesirable as phytometers being discarded. While the plants measured varied from 23 to 65 with respect to water-loss, those employed were chosen from the middle values, viz, 44 to 55, and were grouped in the three batteries in such fashion as to give essentially the same transpiration, namely, 47.8 for the sun, 47.7 for the half-shade, and 47.7 for the full-shade station.

Each battery consisted of 10 plants, which were placed in the containers on June 12, and sealed and weighed the next day, when the batteries were placed in the respective station inclosures. To each were added two containers of the same type, which were filled with soil and employed as checks to test the efficiency of the seal. Ten or more plants of the same

general value were planted in each station in a trench filled with the soil used for the containers. These checks were designed to furnish a record of growth that would permit the recognition of possible abnormal effects due to sealing.

Containers.

Containers were made by soldering a galvanized-iron funnel in the inverted position to a 10-inch pail in such a manner as to reduce the opening to 4 inches. The edges of the opening were rolled over a heavy wire, and the funnel was pierced by half-inch tubes, the one near the opening extending 0.25 inch below the cover and the one near the rim reaching within 0.25 inch of the bottom of the pail. These permitted both top and bottom

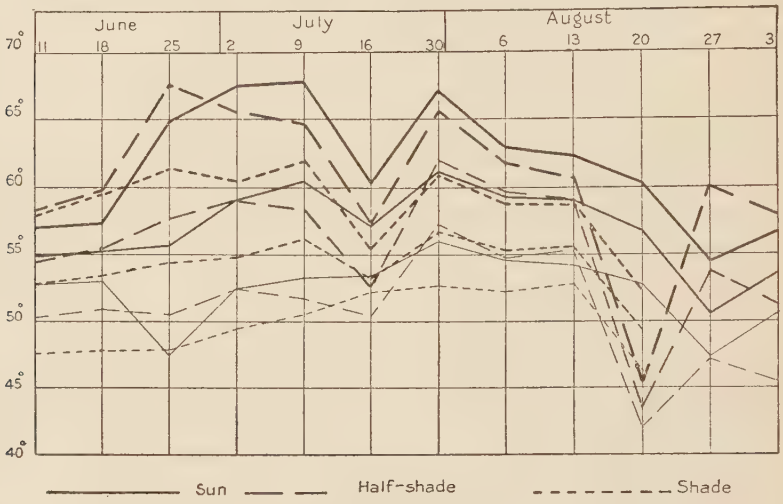


Fig. 25.—Average temperature for day (heavy lines), 24-hours (medium lines), and night (light lines), 1923.

watering and made effective aeration possible by means of drawing air from the longer tube and allowing it to enter through the shorter. The small aperture possessed the advantage of reducing the area to be covered by the seal and correspondingly diminished the danger of cracking, while the rolled rim afforded a firm basis for fastening the cloth of the seal. The conical cover favored filling and firming the soil and hence reduced the subsequent danger of settling and cracking, while the two tubes insured adequate aeration of the soil as well as uniform distribution of the water.

The containers were first filled to a depth of 1 cm. with coarse gravel to serve as a reservoir and to permit the ready movement of air and water, and then with sifted loam, which was well firmed over the entire surface. The plants selected were removed from the 3-inch pots, placed in the containers with the least possible damage to the roots, and sealed by means of a plastocene collar and a cover of wax cloth, as already described. Paraffin melting at 56° was used and proved entirely resistant to the highest temperatures at the shade and half-shade stations, but in the sun it was found desirable to cover it with a thin coat of plastocene clay. The tubes were

closed with rubber stoppers and the containers sunk in the ground to three-fourths their depth.

The phytometers were weighed each week, and the dimensions of stem and leaf measured at the same time. The behavior of the stomata was determined throughout a 24-hour day at several times during the series, and the dry weight and total sugar found at the close. Analyses of the soil-air in the containers were also made at varying intervals, and changes in the structure of representative leaves were recorded at the end of each series.

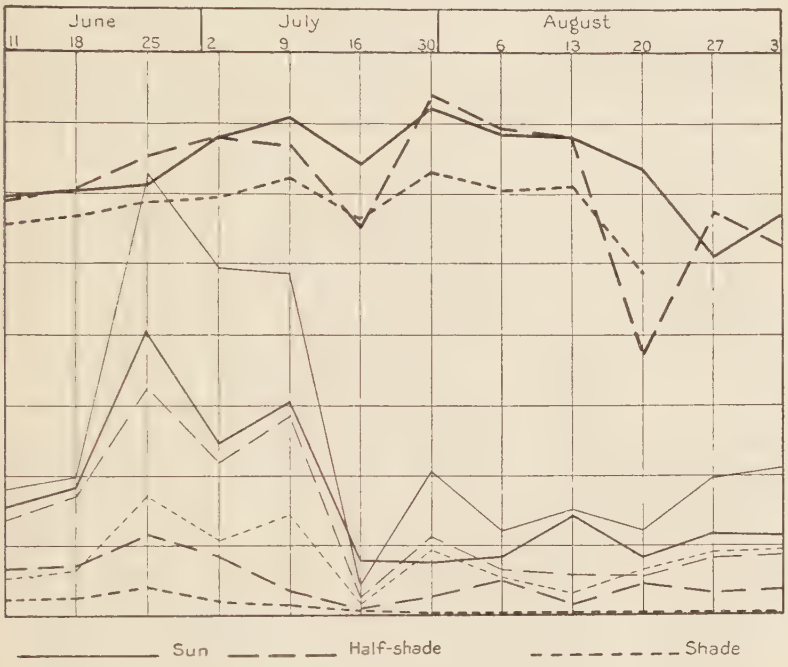


FIG. 26.—Average 24-hour temperature (heavy lines), average daily wind (medium line), and average standard evaporation (light lines), 1923. Each space equals 5 units; the base-line is 0 for evaporation and wind and 25 for temperature.

TEMPERATURE.

Thermographs were maintained at each station in standard shelters placed on the ground. The stations differed less in air-temperature than would be expected, owing largely to continued cloudiness as well as to the greater radiation in the sun. While there was a constant decrease in average temperatures from sun through half-shade to shade, this was only slightly efficient, as the figures indicate. The respective day averages were 63.8°, 62.8°, and 59.8°, the night averages 52.1°, 51.4°, and 49.6°, and the 24-hour averages 57.9°, 56.8°, and 54.6°. Throughout the period the averages were constantly 2° to 6° higher at the half-shade than at the shade station; the relation between the sun and half-shade was less constant, though the former was usually 1° to 3° higher. The differences as well as

the fluctuations were probably due in part to cold-air drainage and variations in the volume and temperature of the brook (fig. 25).

The average weekly soil-temperature at 4 inches was constantly about 10° higher at the sun than at the shade station, the average difference for the series being 9°. This is to be ascribed chiefly to insolation, but it arose in part also from the nearness of the cold brook to the shade station. No ecograph was available for the half-shade station, but frequent readings with the soil thermometer gave intermediate values.

Humidity and Evaporation.

The average day humidity was practically the same in the sun and half-shade, but it was 6° higher in the full-shade. On the contrary, the average night humidity at the sun station was 6° higher than at the half-shade and 3° more than at the shade station, thus making the average 24-hour

Fig. 27.—Average transpiration of sunflowers, 1923.

humidity respectively 6° and 2° higher at the first. The reduced humidity in the sun station during the daytime was obviously a matter of insolation and greater wind movement, while the high night value is probably to be explained by the fact that it was inclosed on three sides by brooks, from which humid air drained into the pocket-like area. The average daily wind movement was greatest in the sun station, intermediate in the half-shade, and least in the full shade, the respective figures being 12.3, 3.3, and 0.99 miles. These were doubtless wholly the effect of the difference in cover. As the anemometers were placed within the station inclosures and as near the plants as possible, the results indicate the actual wind movement effective upon the phytometers.

As usual, evaporation was determined by means of white cylindrical atmometers of the porous-cup type exposed in duplicate at the level of the foliage in each station inclosure. The average evaporation in the sun was practically twice that for the half-shade, and this was nearly twice that for the full-shade, the respective amounts being 18.56, 9.8, and 5.19 c. c. The same relation was maintained throughout the series, showing that the factors for evaporation were constantly different for the three stations (fig. 26).

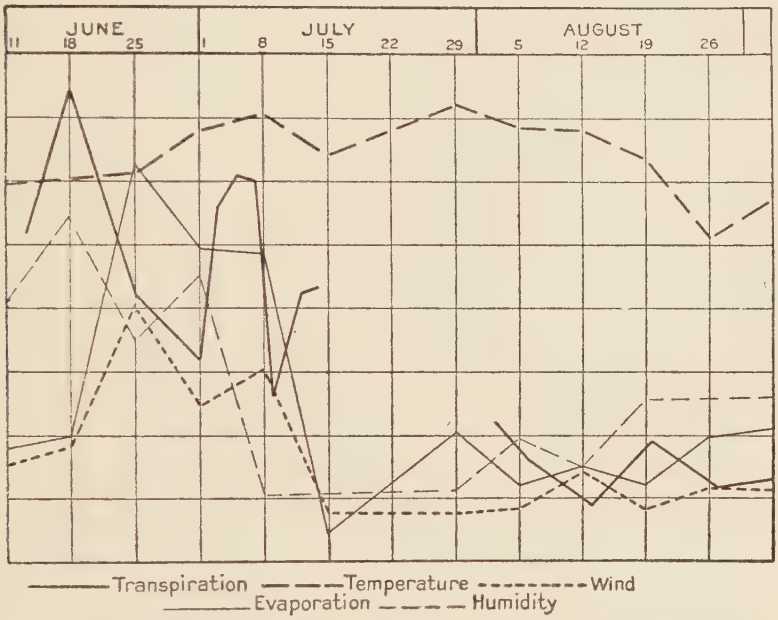


FIG. 28.—Average transpiration of sunflowers, sun station, 1923, compared with factor data. Each space equals 5 units, except for the inverted humidity curve, for which the value is 10; the base-line is 0 for transpiration, and wind and evaporation, and 25 for temperature.

LIGHT.

Chemical photometers, employing a solution of oxalic acid and uranium acetate in accordance with the method of Ridgway (1918) and exposed against a uniform background and at a uniform angle in each station, were utilized for obtaining light values at the three stations on four representative days during the first series. The amount of oxalic acid decomposed during the daylight hours was used as the basis for computing the percentage of light on that of the sun station. As measured by this instrument, the light intensity in the half-shade was 45 per cent and in the full-shade 4.5 per cent of the value at the sun station, values which were too high, as shown by the stop-watch photometers employed in the second series.

Transpiration.

Water-loss was constantly highest at the sun station, and it was usually higher at the half-shade than at the full-shade station, in accordance with the physical factors generally (figs. 27 to 30). The respective values per unit of leaf-area were 25, 12, and 10. The correlation of the transpiration curve with those for the factors concerned or with that of evaporation is nowhere very close, but the correspondence with their composite effect is fairly good.

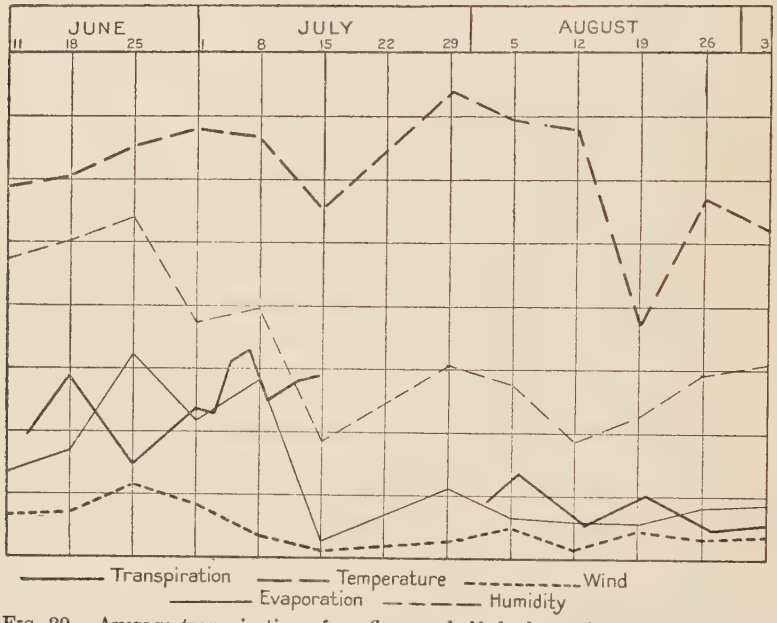


Fig. 29.—Average transpiration of sunflowers, half-shade station, 1923, compared with factor data; values as in fig. 28.

Growth.

As would be expected in consequence of the dense shade, increase in leaf-area was very low at the shade station, while it was correspondingly high at the sun station, the half-shade being intermediate (plate 7). The respective values from shade to sun for the sealed phytometers were 396, 309, and 135 sq. cm. (table 17; figs. 31 to 33). The converse was naturally true of stem-length, the plants in shade and half-shade much exceeding those in the sun, the respective heights being 305, 428, and 203 mm. (fig. 32). Until the last two weeks there was little difference in the height of the phytometers in the two shade stations, but those in the dense shade finally proved too weak to support their weight and some of the tallest became so twisted and bent that they were destroyed by wind and rain before the final readings were made (plate 7). The average stem-diameter varied in the same manner as the leaf-area, being greatest in the sun (7.45 mm.), somewhat less in the half-shade (6.64 mm.), and least in the shade

(4.27 mm.). Thus, the best conditions for growth were found in the sun, as shown by both leaf-area and stem-diameter, but this was more or less obscured by the fact that elongation is more marked in the shade, resulting in taller stems in these two stations. The relation involved is best shown by the ratio between width and length of stem, which is 1 : 27 for the sun, 1 : 64 for half-shade, and 1 : 70 for full shade. While there was considerable variation between the behavior of the sealed phytometers and the unsealed checks, these were in complete agreement as to the response in each station.

Dry Weight and Water Requirement.

The average dry weights of the whole plants as well as of the different organs are entirely consistent for both phytometers and checks in decreasing

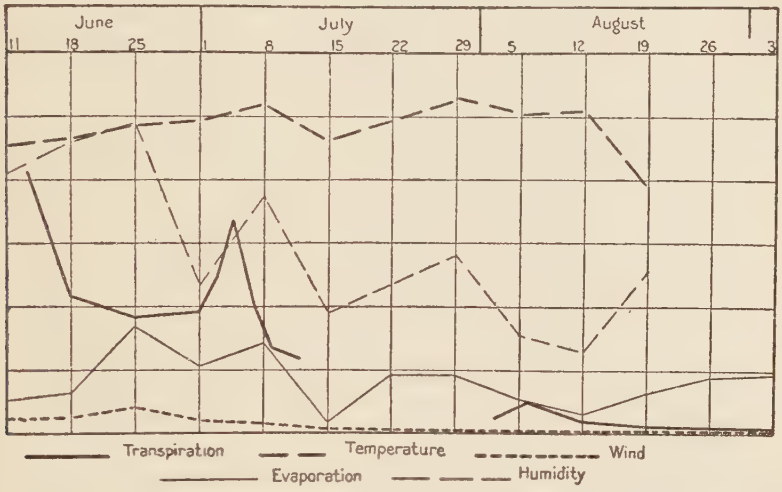


Fig. 30.—Average transpiration of sunflowers, shade station, 1923, compared with factor data; values as in fig. 28.

from the sun to the shade station (table 18). The sole exception occurs in the half-shade stems, in which maximum length has already been noted. This does not hold for the checks, or for the whole plant or shoot, for which the response follows the sequence of the stations. For example, the average dry weight for the shoot in both phytometer and check was 1.64 grams in the sun, 1.06 grams in the half-shade, and 0.27 grams in the full shade. The average water requirement exhibited a similar relation, the respective figures being 805, 486, and 125.

Soil-Air.

The possible effect of the seal under the different habitat complexes was tested by removing 20 liters of air through the long tube at frequent intervals, the first liter being used to sweep the tubing free of residual air. As a further check, the analyses were always made in duplicate. The soil-air in the blank containers was regularly more nearly of the composition of atmospheric air than that found in the phytometer containers. There was

no constant difference in composition at the three stations, the carbon dioxid averaging about 2 per cent and the oxygen about 20 per cent. The former was but little different from the value found in the soil with the free checks, which ranged from 1 to 1.5 per cent at a decimeter deep. As a rule, however, the soil-air from the phytometers and the blank checks departed further from the composition of ordinary air at the two shade stations than in the sun. This was probably a result of the readier ventilation of the containers in the sun, as a consequence of the greater daily fluctuations in temperature.

SECOND SERIES.

Stations and Installation.

The stations and the instrumental installation were the same as for the first series. Seeds from the same lot also were planted on July 5, and after a period of growth the seedlings were transferred to small containers on July 8 and sealed the following day. The transpiration per leaf-area during this time was computed for each of the 118 plants available (table 20). As with the first series, the individuals with too wide a departure in water-loss were discarded; the following were selected, placed in permanent containers on August 2, and organized into equivalent batteries for the respective stations (table 2).

Table 2.—*Transpiration of phytometer plants.*

Sun station.		Half-shade station.		Shade station.	
No.	Amount.	No.	Amount.	No.	Amount.
	c. c.		*c. c.*		*c. c.*
3.....	0.68	1	0.65	2	0.66
6.....	.61	19	.67	9	.64
26.....	.61	20	.60	23	.60
28.....	.60	40	.64	31	.63
50.....	.65	47	.64	49	.63
70.....	.69	53	.69	54	.63
77.....	.62	79	.66	76	.67
99.....	.64	84	.63	94	.69
107.....	.67	101	.63	103	.60
113.....	.67	110	.62	108	.69
Average...	.644	.....	.643	.....	.644

The average leaf-area of the plants in the respective batteries was 25.7 sq. cm. for the sun station, 29.2 for the half-shade, and 28.9 for the full-shade. These areas include the cotyledons, which were removed before placing the plants in the final containers and hence do not appear in the later areas. Since the cotyledons have a slightly different ratio between leaf-product and leaf-area from that of the leaves, and the rate of water-loss differs also, they were removed in the first series and the leaf-product alone considered in the initial selection. In the second series they were not removed until after the selection was made, and in consequence the leaf-area rather than the leaf-product was employed in computing the transpiration rates.

Temperature.

The period of the second series was slightly cooler than that of the first and was marked by an exceptionally large proportion of damp, cloudy weather. The day averages were 2° to 3° lower, but the 24-hour averages were only about a degree less, the values for the shade station being practically identical. The day temperatures averaged 61.6°, 59.6°, and 58.2° from sun to shade, the night 53°, 51.5°, and 51°, and the 24-hour 57.2°, 55.5°, and 54.3°. However, the differences were less constant than in the first series and temperature was correspondingly less efficient in the phytometer behavior during this period (fig. 25).

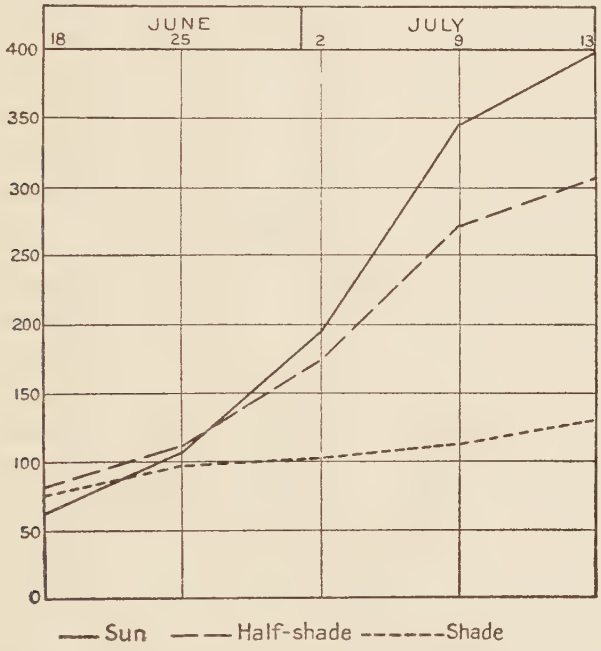


Fig. 31.—Average leaf-area of sunflowers, first series, 1923.

The soil temperatures likewise showed the changed conditions due to almost continuous cloud and rain. The gravel soil of the sun station dropped from 57.3° to 45.5°, while the leaf-mold of the shade fell only 2°, from 54° to 52.2°. The average for the sun was likewise lower than in the shade, but the difference was less than a degree, while the average air-temperature was more than 3° higher at the former. This was in marked contrast to the first series.

Humidity and Evaporation.

The figures for relative humidity are even less significant than in the first series, owing to the fact that the hygrograph is especially erratic during very humid weather in a dry region, as a consequence of the extreme fluctuations within a few hours. While the relation between the half-shade and shade stations is normal, the latter being constantly 5 per cent higher,

there seems no logical explanation of a value 5 per cent higher still in the sun. The chief value of the results lies in showing that the humidities during the second series averaged about 15 per cent higher than for the first. On the other hand, the average wind movement was much lower for this series, being less than half as much for the sun station, where it was 5.1 miles, in contrast to 12.3 miles per day. The amount for the half-shade was 1.9 and for the full-shade but 0.03 mile.

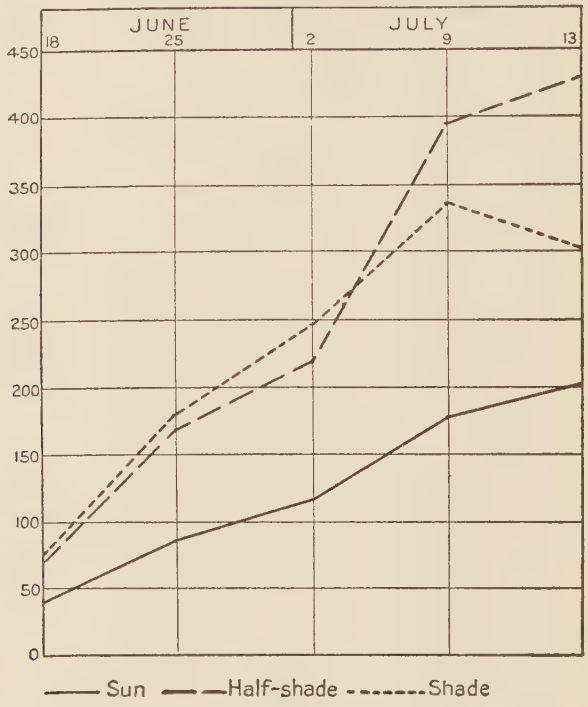


FIG. 32.—Average stem-length of sunflowers, first series, 1923.

The effect of the continuously rainy weather in reducing and equalizing evaporation was marked (fig. 26). The latter was reduced more than half in the sun and half-shade stations, the respective figures for the two series being 18.5 and 8.1 c. c., and 9.8 and 3.9 c. c. The reduction was naturally less in the shade station, viz, from 5.2 to 3.4 c. c., the most significant fact being the close agreement between the two shade stations. In spite of this, the sequence of the three stations was the same in both series, namely, sun, half-shade, and full-shade.

LIGHT.

The light intensities during the second series were measured chiefly by the stop-watch photometer, hourly readings being made in the three stations on a considerable number of days. The average intensity for a 12-hour day on September 2 was 0.4, 0.1, and 0.01 in terms of meridian sunlight on the same day, the relative values for sun, half-shade, and shade being 100 per cent, 25 per cent, and 2.5 per cent respectively. Noon-day values on

August 30 were 0.3, 0.15, and 0.03, while the 7 a. m. readings were 0.25, 0.07, and 0.001, and the 5 p. m. ones 0.15, 0.05, and 0.001 respectively, the greatest divergence coinciding with low altitudes of the sun. The values obtained by means of the chemical photometer were in much closer agreement with these than was the case in the first series, the relative percentages being 100 for sun, 21 for half-shade, and 3 for full-shade (fig. 37).

Transpiration.

The water-loss was not only highest at the sun station as for the first series, but it was also much higher for the half-shade than for the shade. The respective averages per square decimeter of leaf-area were 8, 4.5, and 1.35 grams; the sun station ranged from 1 to 7 grams more than the half-

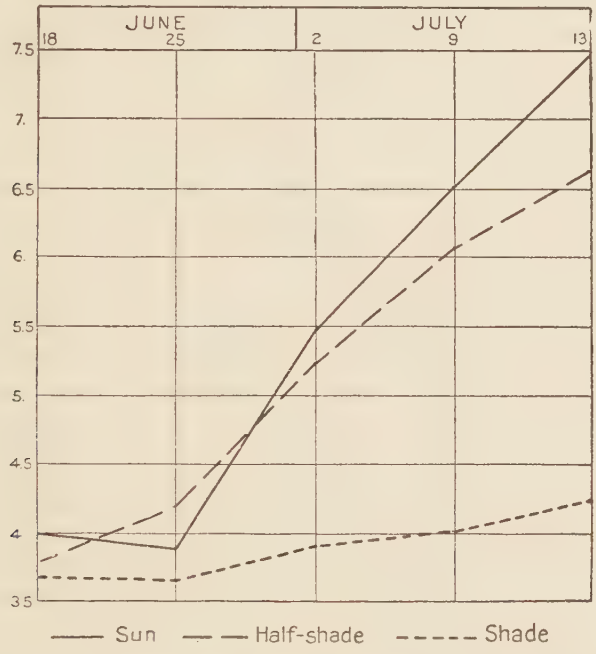


Fig. 33.—Average stem-width of sunflowers, first series, 1923.

shade, and the latter from 2 to 5 grams more than the full-shade (fig. 27). The agreement between the curve of transpiration and that of evaporation in the sun is slight, but there is a general correlation of the former with the curves for humidity and temperature (figs. 27 to 30).

Growth.

When both phytometers and checks are taken into account, the leaf-area was highest at the sun station, least at the shade, and intermediate in the half-shade (plate 8). The percentage of increase was in the same order, the sun station with an average of 55 per cent being twice as high as the shade station with 25 per cent; the checks in the half-shade gave 35 per cent, the low figures for the phytometers being the result of accidents

during the last two weeks (fig. 34). The order for stem-length was exactly the reverse of that for the leaf-area, the shade station being first with 235 mm., the half-shade next with 210 mm., and the sun last with 169 mm. (fig. 35). Again, because of the inverse relation of length and width, the stem diameter varied in the opposite direction (fig. 36), being greatest at the sun station (3.8 mm.), intermediate in the half-shade (3.3 mm.) and least in the full-shade (2.6 mm.). With a single exception, the unsealed phytometers or checks gave higher values than the sealed ones, indicating that the growth of the latter during such a humid period may have been retarded by faulty aeration. However, this is hardly confirmed by determinations of the composition of the soil-air; the amount of carbon dioxid was usually highest in the half-shade, intermediate in the sun, and least in the full-shade. The amount varied from 0.6 per cent to nearly 4 per cent, the blank checks usually yielding about four-fifths as much as the phytometers.

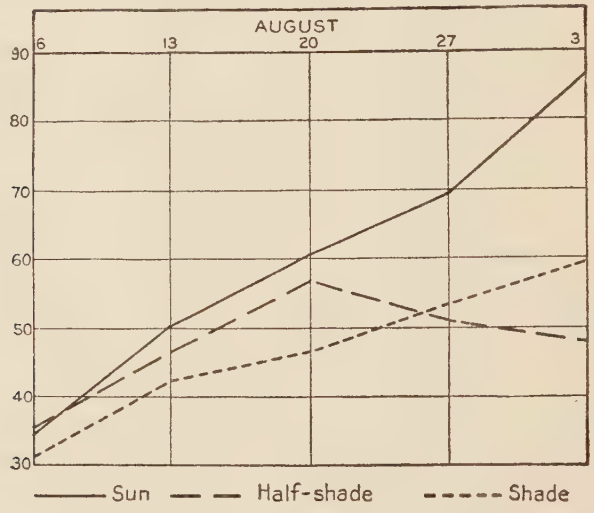


FIG. 34.—Average leaf-area of sunflowers, second series, 1923.

DRY WEIGHT AND WATER REQUIREMENT.

The average dry weights again decreased in the order of the stations from sun to shade, the single exception being that phytometer roots in the half-shade gave a higher value than in the sun (table 18). The respective values for the three stations for the whole phytometers were 1.03, 0.98, and 0.41 grams, and for the check shoots 0.82, 0.37, and 0.26 gram. For the sun and half-shade stations the dry weights were only about half those for the first series, while for the full-shade they were slightly higher, the differences between the stations being consequently much smaller. This is reflected in the water requirement, the demands for water in sun and half-shade being only about a fifth as much as in the first series, and in the full-shade about half as much. The values in the order of the stations were 165, 94, and 59.

SHORT-PERIOD PHYTOMETERS.

The short-period phytometer is one that is operated for a few hours or days in contrast to months or an entire season. It regularly makes use of a single function, such as transpiration, instead of more complex ones, such as growth or yield. Growth and short-period phytometers are complementary, but the latter are so much simpler to install and operate that they have a much wider usefulness for the solitary investigator. Their advantages are many, by virtue of the simpler equipment needed, the briefer period of exposure, and the utilization of single functions. In the matter of equipment, the containers may be smaller and lighter, and hence more easily transported, since the plants do not remain in them for a long period

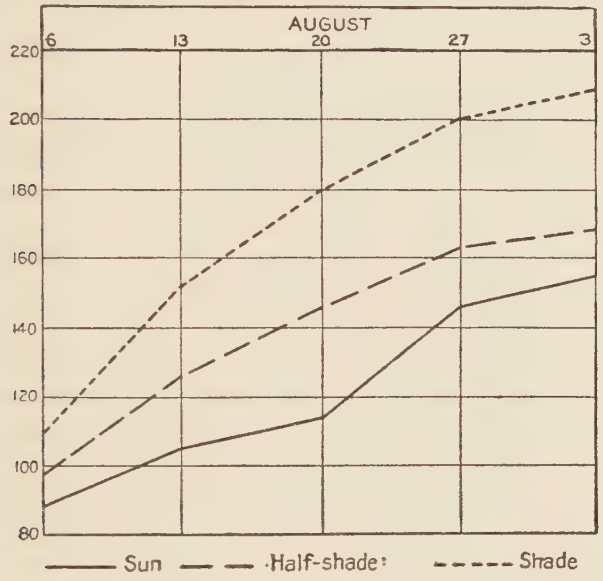


FIG. 35.—Average stem-length of sunflowers, second series, 1923.

and there is less risk of their becoming root-bound or suffering from deficient aeration. Sealing is a much simpler and more certain process, and there is less danger of cracking and consequent absorption of water. The smaller containers make it possible to use smaller and more portable balances and permit greater accuracy in weighing, owing to the reduced load.

The short period is especially advantageous in reducing the chance of accidents of all sorts, particularly from wind and hail. It avoids, or at least minimizes, undesirable changes in the soil-air in consequence of the seal and insures much more normal growth and behavior. It renders it possible to expose the plants to uniform conditions or to a desired set, and avoids the complication of a sudden change in factors. A marked advantage resides in the fact that an abnormal season can not convert an expensive and time-consuming seasonal installation into a more or less complete disappointment, as happened in 1923 at the Alpine Laboratory. The short-period phytometer enables one to employ plants at any stage of

development and to select uniform individuals with the minimum effort; the periods can be regulated so that growth enters little or not at all as a disturbing factor. The periods permit the closest analysis of behavior with respect to any particular function, intervals of a few minutes being as feasible as those of hours or days. However, it must be recognized that the closer the scrutiny, the more exacting the schedule of weighing, or measurement, and factor determinations. Finally, an expensive installation of recording instruments is much less necessary, since simple thermometers, psychrometers, photometers, etc., are fairly adequate.

Applications.

The short-period phytometer can be employed to advantage in any problem not too remote from a base, but its greatest usefulness is where simple functions are concerned rather than growth or yield on a large scale. Even in the latter, however, it is an all but indispensable adjunct of seasonal phytometers, as it permits readier and more exact analysis of the factor-function complex. Within these limitations, it should be utilized in all projects and experiments where instruments are used, since the interpretation of instrumental data must remain misleading, incomplete, or imperfect without phytometers. This means that short-period phytometers are not only necessary, or at least desirable, in all studies in natural or cultural habitats, but also in control experiments in greenhouse or laboratory, and as much or even more in investigations in such applied sciences as agronomy, horticulture, forestry, grazing, etc.

Of all the functions that can be employed as measures, transpiration is by far the most satisfactory; partly because it can be readily and accurately determined without placing the plant under abnormal conditions, and partly because of the basic importance of the water relation as well as its great variability. In these respects, photosynthesis as measured in terms of photosynthate stands next, but this method still leaves much to be desired in the matter of accuracy, while the gas method necessarily modifies habitat factors seriously. This is likewise true of the use of respiration as a measure, and the latter also suffers by having no such direct relation to water or light. Germination may be utilized as a measure of the chresard and of surficial soil-temperatures. Movements have also been employed, as in the case of the opening and closing of flowers, carpotropic movements, the opening and closing of stomata, etc.

Methods.

The selection of species for use as short-period phytometers is determined largely by the object in view and the function to be utilized. In the case of comparative studies, standard plants such as sunflower and beans are to be preferred, while in the accurate interpretation of relations it is often desirable to make use of the very species to be investigated, such as wheat, corn, alfalfa, native grasses, forbs,[1] etc. Special qualities and conditions

[1] The term "forb" is here used for herbs other than grasses in order to afford a clear cut distinction and at the same time avoid an awkward phrase. It is derived from the Greek-Latin root which appears in φορβή and in *herba* (*ferb—).

must often be taken into account likewise; for example, in the present series made toward the end of the season in the montane zone, *Cyclamen* proved the most satisfactory of the several species available, owing to the nature and position of its leaves. The individual plants should be selected on the basis of similarity in behavior as determined by actual measurement under uniform conditions, and in the case of longer series this should be checked, preferably at the end of the experiment. Converting the plant into a phytometer is a much simpler matter than previously indicated, an impervious container of convenient size and a wax seal sufficing in most cases. When the period covers several days or more, especially under strong insolation,

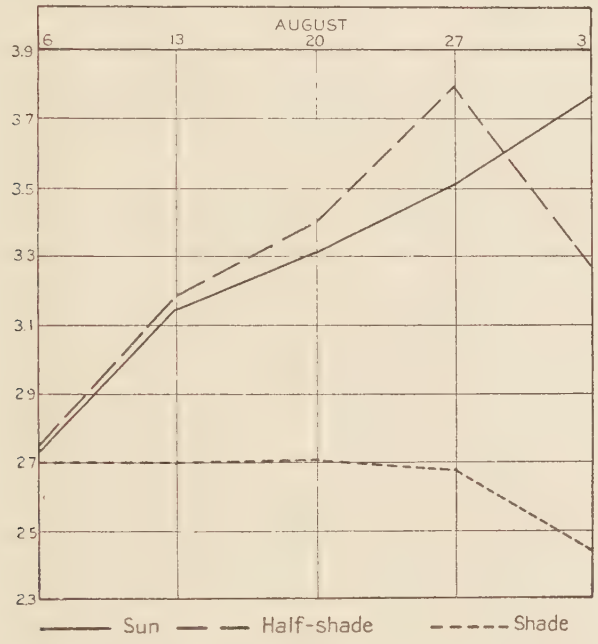


FIG. 36.—Average stem-width of sunflowers, second series, 1923.

a tube is required for watering and aerating the soil. The minimum number of plants for a battery should be 3, though 5 or 10 insure better results. The plants are grouped in each spot in such a way as not to affect each other, but to be under essentially uniform conditions, though when the latter vary considerably it is sometimes better to scatter the plants. When the installation is a large one in distinct habitats, recording instruments are all but indispensable, but in the more intimate analysis with short-period phytometers, the thermometer, psychrometer, atmometer, anemometer, photometer, and geotome suffice in the great majority of cases.

Short-period phytometers lend themselves most readily to hourly determinations through the day or daily ones for a week or so, as well as to the obtaining of morning and afternoon or day and night values. Obviously, intervals of a half-hour or less or 2 to 3 hours are often desirable. When the period is longer than a week or 10 days, the container must be

larger and the phytometer made with greater care, so that it approaches the growth type in many respects. The detailed application of the method is of the widest, ranging from transpiration and other measurements in distinct climatic or seral habitats at the one end to the detailed analysis of minute habitat areas at the other. It has been employed for measuring the efficient factors in sun and shade, at different altitudes, on opposite slope-exposures, in different forest layers, in the shade or in the crown of different shrubs and trees, above various covers or soil surfaces, at different angles of slope, etc. In short, it gives results of value wherever factor differences exist.

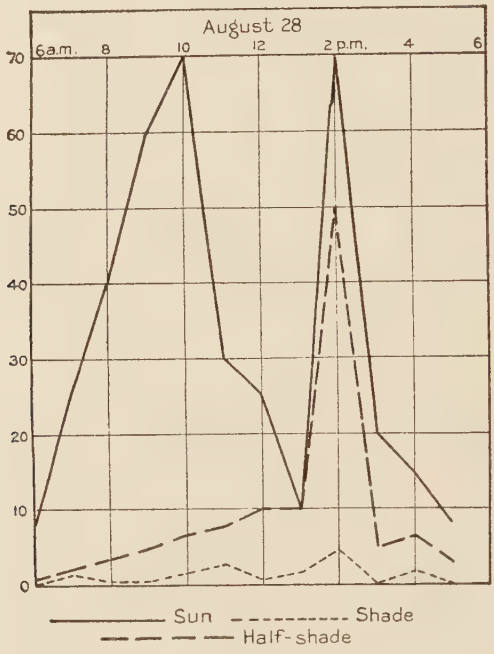
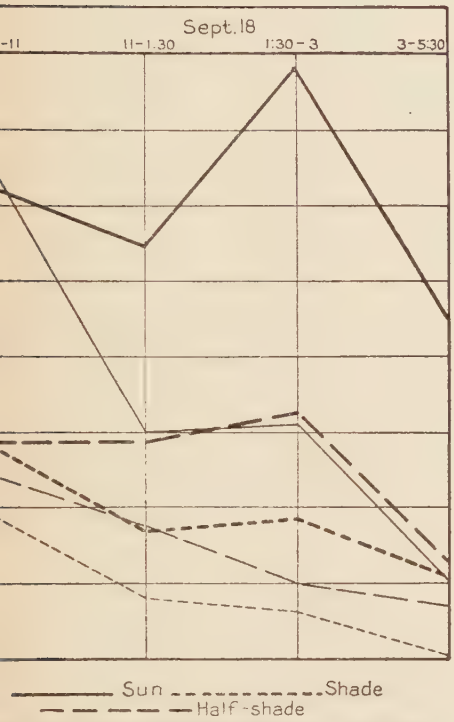


FIG. 37.—Light intensity in terms of meridian sun, August 26, 1923.

INSTALLATION FOR 1923.

The continuously rainy summer interfered with the experiments planned for short-period phytometers, and favorable sunny conditions were available only in September and near the close of the season. This limited the choice of species in the first place, and practically all of these except *Cyclamen* were eliminated by snow and hail. The thick, semi-fleshy leaves of the latter made it especially adapted to late-season studies, and they possess the further advantages of being nearly entire, horizontal, and on much the same level. The instrumental installation was maintained in the three major phytometer stations, and this served also as a background for readings by means of simple instruments in the temporary stations. The plants were transferred to impervious pots, watered and sealed, and then given a day or two for adjustment before being used. Plants of moderate

size were selected, particular care being taken to see that all the leaves were normal and freely exposed. The pots employed were 4-inch paper ones previously coated with paraffin and sealed by means of a collar of plastocene clay about the plant and a layer of paraffin melting at 56° over the soil surface. Weighing was done on a torsion balance with a capacity of 4.5 kg.; this was kept indoors in a neighboring laboratory to avoid various minor disturbances. In the temporary stations readings of light and tem-



IG. 38.—Average transpiration per leaf product (light lines), and average evaporation (heavy lines); short-period phytometers, September 18, 1923.

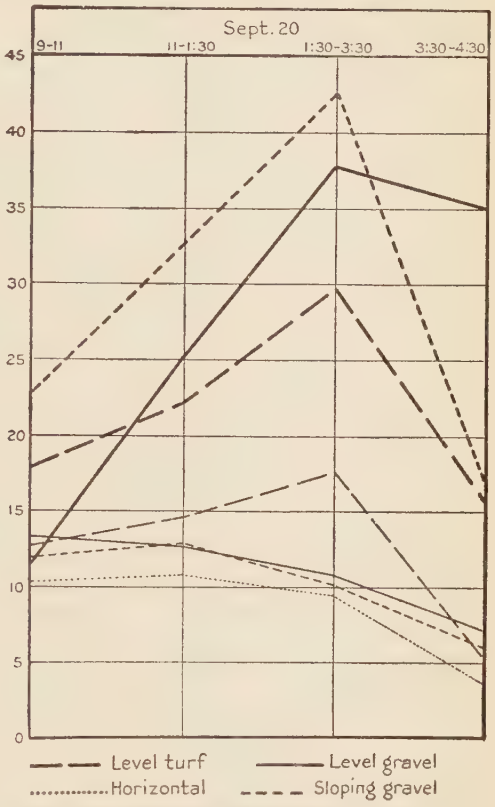


FIG. 39.—Average transpiration per leaf product (light lines), and average evaporation (heavy lines); short-period phytometers, September 20, 1923.

perature were made at frequent intervals, and evaporation was determined by means of white cylindrical atmometers run in duplicate, the readings being averaged and reduced to standard.

SUN AND SHADE.

Batteries of four *Cyclamen* phytometers were installed in each of the three main stations, sun, half-shade, and shade, on September 16. The plants were exposed at 11 a. m. after being weighed and were removed and weighed again at 4 p. m. The average hourly loss divided by the leaf-product gave the relative values of 37 for the sun, 16 for the half-shade, and 9 for the full-shade station, the respective percentages being 100, 44, and 24

(table 21). The same batteries were again exposed on the 18th and weighings made at four intervals from 9 a. m. to 5^h30^m p. m., from which the hourly loss was computed. The hourly loss was again more than twice as great in the sun as in the half-shade and about twice as much for the latter as for the full-shade (fig. 38; table 22). In general, a similar relation obtained between the evaporation at the three stations; this was in harmony with the light and temperature readings, with the exception that the shade station was slightly warmer than the half-shade.

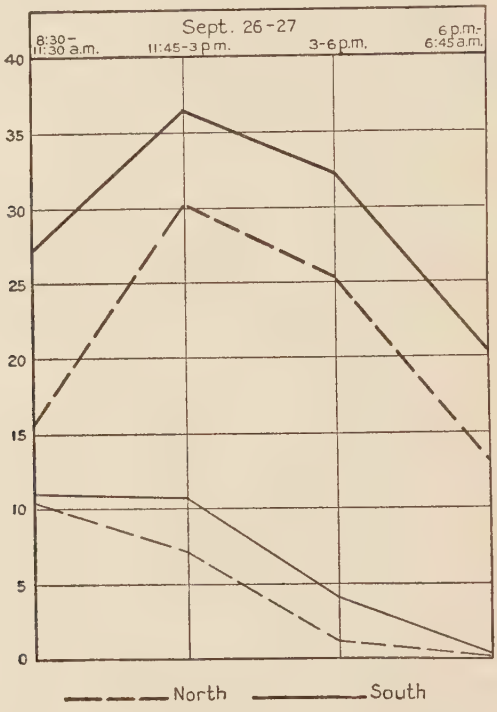


FIG. 40.—Average transpiration per leaf product (light lines), and average evaporation (heavy lines); short-period phytometers, September 26–27, 1923.

On September 21 all the phytometers were placed on level gravel soil in full sunshine from 9^h40^m to 11^h40^m a. m. to determine the individual variability and to permit grouping them in batteries of similar average loss (table 24). They were then exposed in full sun, half-shade with many sun-flecks beneath birch (*Betula occidentalis*), and deep shade under spruce (*Picea engelmanni*), where there were no sun-flecks and practically no ground cover. The respective values were 120, 48, and 11, the percentages being 100, 39, and 9. Evaporation was relatively more marked in the shade stations, the respective percentages being 55 and 29. This is readily explained by the fact that the differences in temperature between the three stations were small, while the light intensity decreased greatly.

Surface, Slope, Exposure, and Altitude.

Four batteries of *Cyclamen* phytometers were installed within a few yards of each other in as many different situations on September 20. Two were placed on the level, one in a short bluegrass turf, the other on bare gravel; the other two were put on a bare gravel-slope facing the south. In one the leaves were maintained in the usual horizontal position, while in the other the plants were shifted each hour to keep the leaves at right angles to the sun's rays. An unexpected disturbing factor entered by virtue of the fact that the phytometers on the bare gravel wilted somewhat during the middle of the day, and this resulted in a decrease in the rate of transpiration. Hence, while the phytometers gave conclusive evidence of the more xerophytic conditions above the gravel, this appeared in the figures for transpiration only during the first and last period (fig. 39; table 23). On the contrary, evaporation above the gravel was slightly lower than for the turf during the first period, but it then rose more rapidly and was more than twice as great from 3^h30^m to 4^h30^m p. m. The phytometers with the leaves at right angles to the sun's rays gave a consistently higher water-loss throughout the day, the divergence from the horizontal leaves naturally becoming greatest in the last period, when the angle of incidence was smallest. Evaporation was highest on the gravel slope, owing to its south exposure, but it also fell off markedly during the last period.

Short-period phytometers of *Cyclamen* were run on north and south slope-exposures of Engelmann Canyon at the Alpine Laboratory from 8^h30^m a. m. September 26 to 6^h45^m a. m. September 27, the distance between the two stations being about 100 yards. As was to be expected, the south exposure was found to be both drier and warmer than the north throughout the day and night, though the temperature difference at night was naturally much smaller. The general agreement between temperature, light, and evaporation on the one hand and transpiration on the other was good, the curves of the latter being flattened by the fact that maximum light intensity came much earlier in the day than the maxima for temperature and evaporation (fig. 40; table 25).

On September 22, batteries of *Cyclamen* phytometers were exposed simultaneously in full sunshine at the Alpine Laboratory, 8,100 feet, and at Windy Point on Pike's Peak at an altitude of 12,500 feet. In spite of considerable differences in temperature, the transpiration and evaporation were nearly the same, being only slightly greater at the lower elevation. This is in contrast to earlier studies (Clements, 1908), which gave higher values on alpine summits, evidently in response to reduced air-pressure, and is probably to be explained by the prevalence of snow at this late date.

RELATED APPLICATIONS OF THE PHYTOMETER METHOD.

SLOPE-EXPOSURE STUDIES.

The marked differences of vegetation on opposite slopes have often been noted, but no comprehensive and thoroughgoing analysis of the physical factors, growth relations, and community behavior had been made before the present study (Clements and Lutjeharms, 1921–1923; Lutjeharms, 1924). In mountain regions of the West in particular, the difference between northerly and easterly slopes on the one hand and southerly and westerly ones on the other may amount to a whole climax, the dry-warm slope being subclimax to the general climax or the moist-cool slope exhibiting

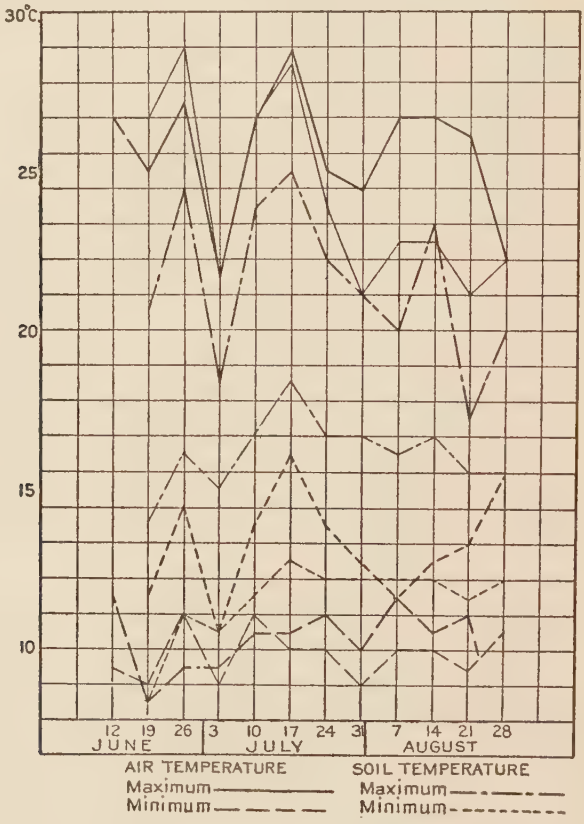


FIG. 41.—Comparison of air and soil temperatures on north (light lines) and south (heavy lines) slope-exposures, Alpine Laboratory.

a postclimax (Plant Succession, 109; Plant Indicators, 88). Such relations are fundamental to the investigation of changes of climate and vegetation, and hence to the phylogeny of climaxes. They have come to play an increasingly important part in the comparative evolution of formations and

associations, and this has rendered it advisable to employ definite terms for the two types of slope-exposure, especially since the terms drawn from direction are often awkward and their significance is reversed for the northern and southern hemispheres. Regardless of exposition, the dry-warm slope is designated the *xerocline* (ξηρός, dry; κλίνος slope) and the moist-cool slope the *mesocline* (μέσος, mid, hence moist).

Installation.

An unusually favorable opportunity for slope-exposure studies was afforded by Engelmann Canyon, in which the Alpine Laboratory is situated. This is a long, narrow canyon on the east slope of Pike's Peak, extending from the foothills at 7,000 feet to an altitude of 9,000 feet. In consequence,

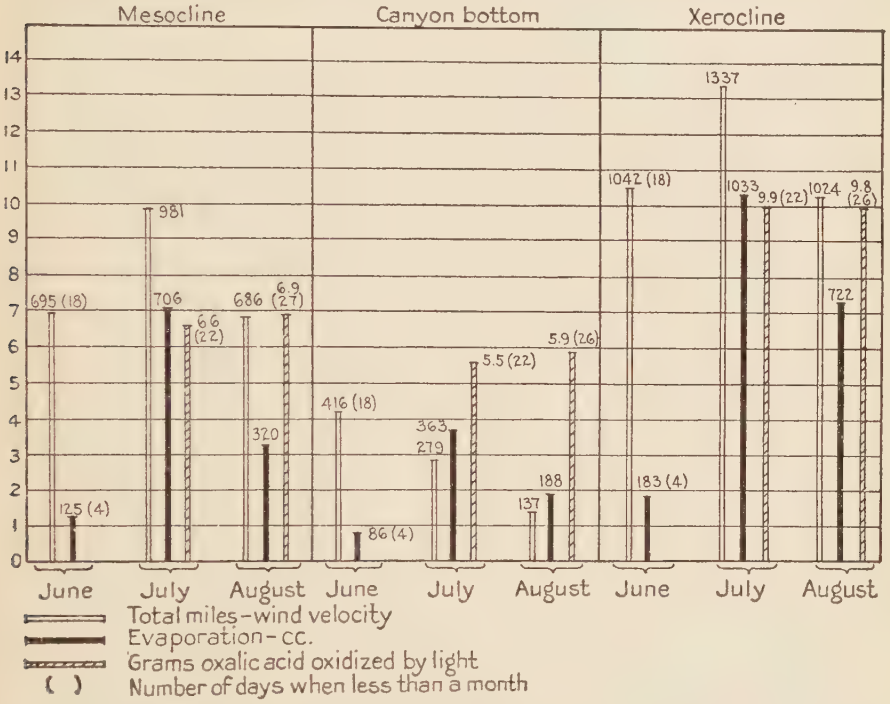


Fig. 42.—Monthly value for wind, evaporation, and light in slope-exposure transect.

it has constituted a highway for the movement of grassland and plains species upward along the xerocline during dry phases of the climatic cycle and of montane and subalpine ones downward during wet phases. In the vicinity of the Laboratory to-day, the north exposure is covered with a practically pure forest of Douglas fir (*Pseudotsuga mucronata*), while the south exposure is a mictium of grassland and chaparral, dotted with yellow pines (*Pinus ponderosa*), scattered Douglas fir, and occasional limber pines (*Pinus flexilis*). Extensive thickets of chaparral, consisting chiefly of *Quercus, Holodiscus,* and *Prunus,* occur in the more stable areas, but for the most part the slope is occupied by an open bunch-grass community of *Elymus triticoides, Muhlenbergia gracilis,* and *Andropogon scoparius,* with

relict areas of *Agropyrum glaucum, Bouteloua gracilis,* and *Elymus canadensis,* and numerous subdominants from the plains.

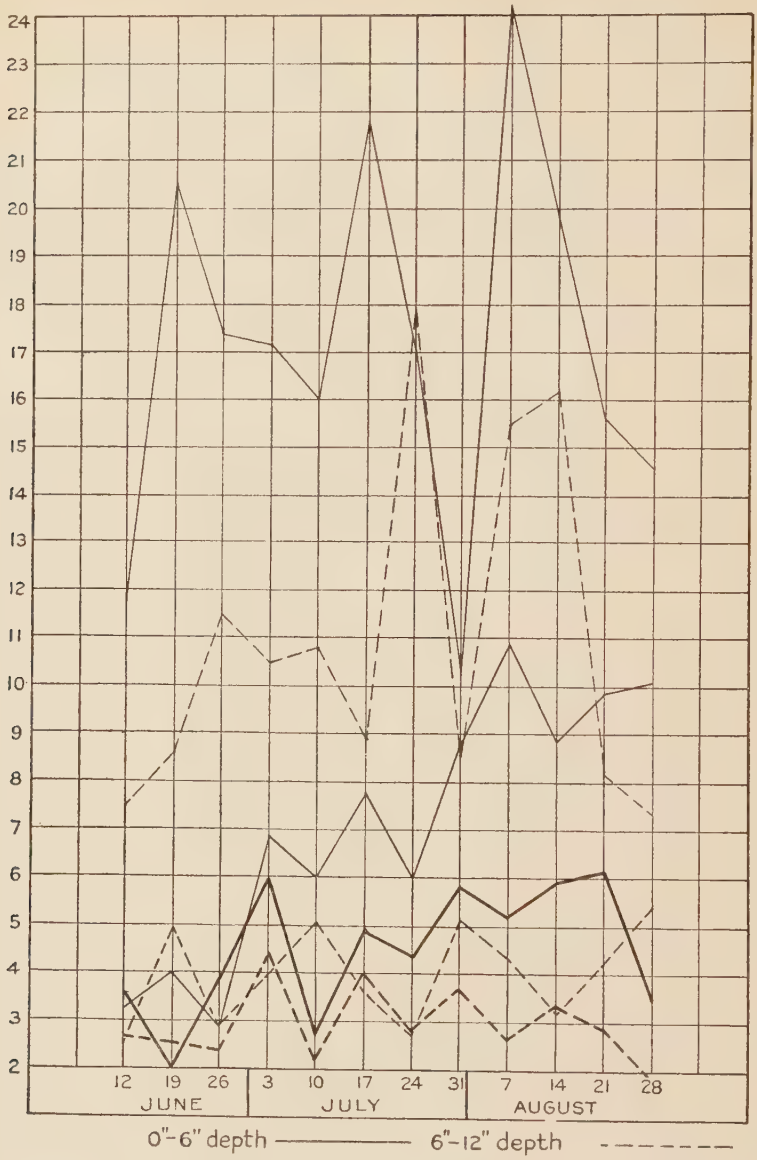


FIG. 43.—Comparison of holard percentages in slope-exposure transect; south slope-exposure (heavy lines), north (medium lines), bottom of canyon (light lines).

Two stations were located directly opposite each other, at a height of about 500 feet above the bottom of the canyon, where the third station was installed near the brook. Complete batteries of instruments were placed in each of the stations and continuous records obtained of the following

factors: (1) air-temperature, (2) soil-temperature at depths of 4 and 12 inches, (3) relative humidity, (4) evaporation, (5) wind, (6) light intensity, (7) precipitation, and (8) holard. Several native and cultivated species, including some shrubs, were employed as phytometers, but the best results were obtained with the sunflower. The functions utilized were transpiration, photosynthesis, and growth, in terms of stem-height, diameter, leaf length and width, dry weight, and water requirement. The detailed results of the investigation are now being published (Lutjeharms, 1924), and a brief summary will suffice here.

Summary.

The efficient factors gave the following differences for the xerocline in comparison with the mesocline (figs. 41 to 43).

Air-temperature (average of maximum and minimum readings)	+ 2°
Soil-temperature (average of maximum and minimum readings)	+11°
Average daily soil-temperature at 12 inches	+16°
	p. ct.
Light, evaporation, and wind, each approximate	+ 50
Average humidity	− 6
Holard at 0 to 6 inches	− 36
Holard at 6 to 18 inches	− 26

The transpiration and growth of phytometers during the entire season gave the following values for the xerocline (plate 9; figs. 44, 45):

	p. ct.
Average leaf-area per phytometer	+ 14
Average stem-diameter per phytometer	+ 10
Average stem-height per phytometer	− 25
Average dry-weight per phytometer	+ 75
Average transpiration per phytometer	+ 82

For phytometers grown half as long and during the latter part of the summer, the values were as follows:

	p.ct.
Average leaf-area per phytometer	+ 71
Average stem-diameter per phytometer	+ 10
Average stem-height per phytometer	− 13
Average dry-weight per phytometer	+ 38
Average transpiration per phytometer	+130
Average carbohydrate reserves in milligrams of dextrose	+ 32

The preceding instrumental and phytometer results make it clear why the south slope-exposure is covered with the scrub and grassland dominants of foothill and plains, while the north one is dominated by the characteristic montane forest of this climatic zone. They also serve to explain the reason for the dry-phase invasion along the xerocline and the wet-phase movement down the mesocline, as well as in the bottom of the canyon.

Transpiration and Growth in the Grassland Climax.

PHYTOMETER BATTERIES.

In order to obtain further light as to the climatic differences of the major stations in terms of functional response, a special investigation was made of transpiration and growth (Clements and Weaver, 1924). Plants of *Helianthus annuus, Avena sativa, Elymus canadensis,* and *Acer negundo* were grown from seed or transplanted as seedlings into sheet-metal containers of appro-

Fig. 44.—Average dry weight and transpiration of phytometers in slope-exposure transect; south slope-exposure (heavy lines), north (medium lines), bottom of canyon (light lines).

priate shape and sufficient size to accommodate the root systems throughout the duration of the experiment. After the plants were well established, the leaf-area and the weight of plant and container were determined. They were then installed at the several stations, together with a complete battery of instruments, for a period of 14 days, and measurements made of transpiration and growth in terms of increased area. The considerable differences in altitude, and hence in seasonal development, made simultaneous studies undesirable, and consequently the periods of observation were successive. This was also imperative because of the time and effort involved.

The individual plants of sunflower and box-elder were placed in cylindrical galvanized-iron containers 5 to 6 inches in diameter and 9 to 10 inches deep, filled with rich loam soil tamped firmly in place. A layer of 0.5 inch of coarse gravel in the bottom of the container covered an exit tube, consisting of an automobile tire valve-stem with the inner end cut off and covered with a fine copper gauze soldered in place. The core of each tube had been removed. The tube was soldered in place with the threads projecting through the wall of the container, so that an exhaust-pump could be attached for aerating the soil. The tube also assisted materially in watering the plants, the usual cap preventing loss during the intervals. The soil was well screened, brought to an optimum holard, and weighed at the time of filling the containers. By restoring the containers to their original weight from time to time, the holard was maintained at the desired level. To

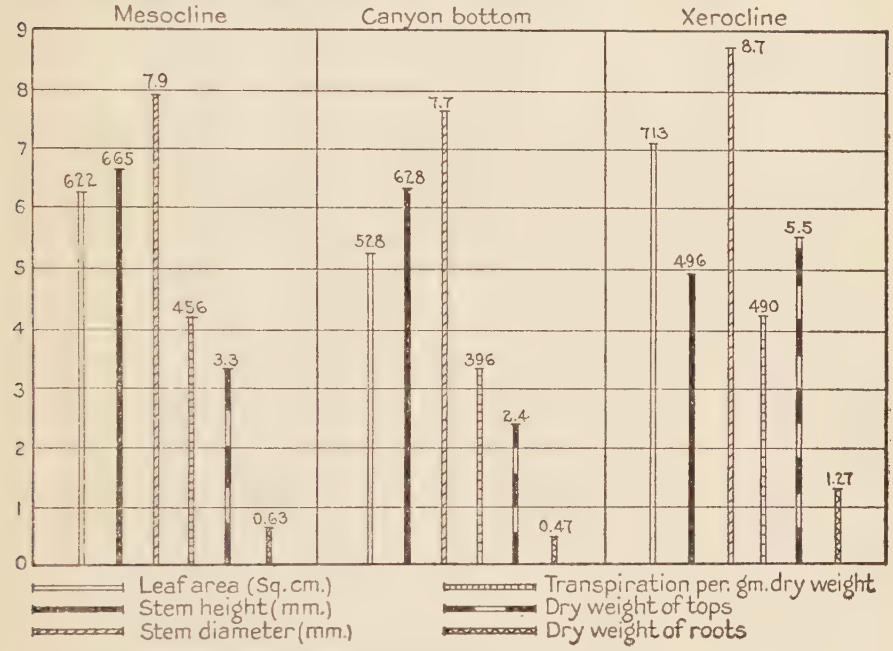


Fig. 45.—Comparative growth and dry weight of phytometers in slope-exposure transect.

prevent loss other than by transpiration, the containers were furnished with a sloping metal top provided with a circular opening, with the edges reamed upward, and large enough to receive a cork 2.5 inches in diameter. An effective seal was formed by boring a hole large enough for the plant stem, splitting the cork and fitting it into place after padding the sides of the opening with a little cotton. The seal was tested by a check container without a plant but fitted with a wooden peg to simulate the plant stem. During the period of 14 days this did not lose water in an amount sufficient to be detected by a balance sensitive to 2 grams under a load of 7 kg.

The containers for wild rye and oats were similar to those already described, except for the tops, which were furnished with a slit 5 inches long

and 1 inch wide. The edges of the metal cut in making the slits were turned down into the container about a quarter of an inch on each side and a half-inch at the ends of the slit. These furnished supports for narrow strips of shellacked oak, which were held in place by thin wedges of similar material at each end. These were put in place after the containers had been filled and the soil pressed firmly under the metal tops. They were then coated with shellac so that no openings remained except between the wooden strips, which narrowed the slit to about 10 mm. The seeds were planted through this opening, which was nearly filled with soil kept moist by frequent watering. After the plants came up, the remainder of the opening was filled with sand level with the top of the wooden strips. The containers were provided with felt tops, cut to fit around the slits, and sunk level with the soil. The efficiency of the sand-mulch in preventing water-loss was found to be high, only 6 grams escaping in a period of 2 weeks. Twelve plants of average size were selected from the several containers and

TABLE 3.—*Transpiration and growth at the three stations.*

Species.	Water-loss per sq. dm.			Increase in area.			Rate of growth, based on actual increase in area		
	Lincoln.	Phillipsburg.	Burlington.	Lincoln.	Phillipsburg.	Burlington.	Lincoln.	Phillipsburg.	Burlington.
	gm.	*gm.*	*gm.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Sunflower	145	225	214	409	1,477	4,097	854	860	998
Wild rye	72	199	218	239	257	163	410	549	140
Oats	99	178	212	279	246	694	1,155	796	510
Box-elder	85	159	137	85	162	220	52	161	370
Average	100	190	195	253	535	1,294	618	591	504

the leaf-area determined. From this, and the number of plants in each container, the initial area of the group of plants in any container was calculated. The final area was determined in a similar manner. This method was used because it was quite impossible to determine the total area of the plants in place, as could be done with the dicotyls.

Owing to cool, wet weather the plants grew slowly, except during the last week of May. They were kept covered during rains and at night, watered from a burette, and aerated from time to time. To keep the metal containers from heating the soil, they were surrounded by sand and the top covered by a collar of felt about a centimeter thick, held in place by strips of adhesive tape. On June 1 the leaf-area was determined by means of solio prints and the planimeter, corks were inserted, and the containers (with collars removed) brought back to their initial weight after they had been transported to the stations in the high prairie at Lincoln, and at Phillipsburg and Burlington. Here they were placed in the soil and thoroughly covered after the collars had been replaced, the exposed plants being sheltered during rains.

After the 14-day period of the experiment, following final weighings, the number of parent plants and number of tillers in each container was ascertained. Eighteen specimens of each group were then selected and their areas determined. From these data the final areas were calculated.

This series proved a disappointment in so far as normal climatic relations were concerned, owing to the wholly exceptional weather. The amount of sunshine at Lincoln was little more than half that at the other stations, while the air-temperature averaged 10° lower and the soil-temperature ranged from 11 to 15° lower. The average humidity was 15 to 18 per cent higher and the evaporation but a third or a fourth of that at Phillipsburg or Burlington. Hence, it is easy to understand why the increase in area was twice as great at Phillipsburg and more than four times as great at Burlington, though the normal relation is suggested by the rate of growth

TABLE 4.—*Environmental conditions at the three stations.*

Station.	Approximate hours sunshine.	Average day temperature.	Soil temperature.	Average day humidity.	Average daily evaporation.	Wind, miles per hour.
		° *F.*	° *F.*	*p. ct.*	*c. c.*	
Lincoln.....	39	70.1	62 to 71	75	8.4	3.6
Phillipsburg...	75	80.6	74 to 82	60	25.5	3.3
Burlington....	71	80.0	73 to 86	57	35.4	3.4

based on the actual increase in area and by the order of water-loss at the three stations. Thus, while the plant responses are in agreement with the physical factors for the respective fortnights concerned, it is obvious that entirely comparable results could be insured only by dealing with the growth season for each species. An adequate record of transpiration and growth for such a period at stations widely separated demands at least one resident investigator for each station, and such studies must await the future.

COMMUNITY PHYTOMETERS.

SOD-CORE PHYTOMETERS.

One of the major tasks of quantitative ecology is to determine the functional responses of plants when grouped in communities. While much light can be obtained by the use of individual plants under control in the field, in the form of standard phytometers, these differ essentially in their soil and competition relations from plants growing together in the actual cover. Hence, the task is to maintain these natural relations of the community and at the same time to secure a degree of control that modifies the efficient factors little or not at all. In the case of transpiration, for example, these requisites can be met only by weighing, as all other methods modify the physical factors to an undesirable degree. The method that maintains the soil and community relations with the minimum disturbance is the soil-block, which was first employed for determining the chresard in the field (Clements, 1904, 1905). This requires only such slight modifications as those of size and form to become applicable to all problems in which an undisturbed soil-root core is indispensable (Weaver and Crist, 1924).

In consequence, the first objective was to perfect the soil-block method so that it could be used in the field with both convenience and accuracy. Because of its importance in the grassland climate, the chief function to be measured was transpiration, though chresard and aeration can be studied with something of the same readiness. In the present case the transpiration from representative cores was followed in the proper climate of each association, but it is evident that the containers can be moved or exchanged between different edaphic or climatic stations and thus serve as reciprocal phytometers. This permits the determination of the transpiration behavior of each climax in its own climate in terms of adjustment and adaptation and at the same time affords a basis for comparing adjacent climaxes. A further use of fundamental value arises out of the rainfall relation. The method of the soil-core not only makes it possible to trace the complete water cycle of rainfall, holard, evaporation, and transpiration, but also to estimate the extent to which the vegetation of each region may furnish the water-vapor for its own rainfall (Clements, 1923). Finally, it also opens up a new field in the functional relation of roots to the soil as an actual structure, which shows striking differences from climate to climate, as well as from one local habitat to another.

Methods.

A steel cylinder 12 inches tall and with an inner area of 1 square foot, the lower edge of which was sharpened, was driven into the grassland soil to a depth of 4 inches. Care was taken to cut off none of the leaves belonging to the plants in the square foot selected, which was chosen with a special regard to its representative structure. The cylinder was then carefully removed, leaving the column of soil intact, and replaced by one of heavy galvanized iron 3 fect long and reinforced at both ends by a heavy wire over which the metal was turned back smoothly. After starting a row of these cylinders at distances of 8 inches, a trench 2 feet wide was dug around them to a depth of over 3 feet. In this process no soil was removed within 3 or 4 inches of the cylinder. As the trench was deepened, the columns of soil were carefully pared away with large knives in such a manner that the cylinders could be forced down under considerable pressure from above. By shaping the column for a few inches in front of the descending cylinder, it was possible to force the latter into place over a tightly fitting soil-core to a depth of 3 feet. The columns were then undercut and smoothed off level with the lower end of the cylinder. A loose-fitting metal bottom with the edges 2 inches deep was placed over the end and the entire container was then weighed on a portable Fairbanks scale sensitive to one-fourth pound.

In the meantime a trench sufficiently wide and deep to receive the cylinders in an upright position had been dug in a nearby area, care being taken not to cover the grass with soil. The containers were lowered in the new trench and slid into place on a plank in the bottom, after which the bottoms were made water-tight by means of a measured amount of hot wax of the usual composition. The trench was then filled with soil and pieces of sod were fitted around the tops so that the surface conditions would be essentially normal. The trenches were selected so that the

surface-water would readily drain away from them, and in addition the plants were covered by wooden roofs whenever rain was actually falling. This was imperative because of the varying interception of rainfall by the different vegetation in the several containers. In the case of the cultivated crops, oats and millet, the usual type of bottom was replaced by one 3 feet deep, owing to the difficulty of selecting a proper slope for drainage. In order to determine the amount of water evaporated from the cultivated soil, the plants were removed from one container in each field. In another the natural grasses were left in place after having been killed by the addition of a measured amount of boiling water (plate 10A).

TABLE 5.—*Comparison of factors and average water-loss.*

Station.	Dominant grasses.	Date of experiment.	Approximate sunshine.	Aver. day temp.	Aver. day humidity.	Aver. daily evaporation.	Aver. daily loss from sq. foot of cover.
			p. ct.	° *F.*	*p. ct.*	*c. c.*	*lbs.*
Burlington	Bulbilis, Bouteloua, Agropyrum	July 5 to 20.	71	80	57	35.4	0.96
Phillipsburg	Bouteloua, Andropogon	June 18 to July 3.	75	80.6	60	25.5	1.33
Lincoln	Andropogon, Stipa, Koeleria, Bouteloua	July 24 to Aug. 8.	47	79	80	22.0	0.85

From time to time, depending upon the weather and the needs of the plants, water in measured amounts was slowly added to all the containers, and as a result there was little shrinkage of the core from the sides of the container. None of the plants died, and even those near the edges gave no signs of wilting, demonstrating that the roots in the core supplied abundant water for transpiration. Much care was exercised in watering, so that there was little or no runoff down the sides of the core. This was accomplished by pouring the water on slowly and pressing the moist soil firmly against the cylinder wherever the contact was not complete. At the end of the period the containers were again weighed and the losses calculated. At the end of the experiment the vegetation was carefully removed at the soil surface by means of a hand grass-clipper. The dense foliage of former years was carefully separated from the living plants, the latter oven-dried at 60° C., and weighed.

RESULTS.

As in the case of water-loss from the phytometers, the exceptional weather of the summer obscured the normal climatic response of the sod-cores. When the physical factors and the type of vegetation are taken into account, it is clear why the low short-grass cover at Burlington in the driest climate transpired less than the mixed prairie at Phillipsburg in a moister atmosphere and more than the luxuriant true prairie at Lincoln in a much more humid climate. Thus again, while the use of sod-cores contributed no clear-cut evidence as to the relation of the three climaxes and their climates, it does demonstrate the value of the method and what can be expected of

it when employed through a series of years. The losses from the three crops, while of interest, have no comparative value, since a different species was used in each station; they are distinctly helpful, however, in showing the similarity in the behavior of the native cover and representative crops for each station and in potential importance for the rainfall of each region. However, in the future development of the method, it is obvious that the same dominant and the same crop should be employed throughout the series of stations, and this should involve the reciprocal transfer of sod-cores and crop-cores between the three stations.

FIELD-PLOT PHYTOMETERS.

The field-plot and cut-quadrat phytometers have much in common when the latter is used for cultivated plants, the chief difference being the greater size of the former. The field-plot type was utilized in 1922 and 1923 for measuring the conditions in dry-land farming and in irrigated fields in terms of root behavior and yield. The installation was made at Greeley, Colorado, in plots of one-thirtieth acre in fully irrigated, partly irrigated, and dry land. The crops employed were alfalfa, spring wheat, sugar beet, potato, and yellow dent corn. Complete records were kept of the usual factors, except wind, and the holard was determined weekly to a depth of 4 feet and at longer intervals to the depth of root penetration, 5 to 9 feet. As the dry-land and irrigated areas were only about a mile apart, the general climatic conditions were identical and the soil was similar, the efficient differences arising out of the irrigation. The development of the root system was traced at several intervals during the growing season, growth of shoots measured from time to time, and the yield determined at the end (Jean and Weaver, 1923, 1924).

In every case the root development and habit were found to respond closely to variations in the holard, and the crops with the most extensive root systems to give the largest yields. The general root behavior may be illustrated by wheat, the roots of which spread more widely in the surface soil owing to showers, but died below 2 feet in dry soil, the corresponding penetration being 3 feet in lightly irrigated and 4.3 feet in fully irrigated soil. The plots were at first equally moist in 1923, and the root systems were alike; because of greater rainfall the penetration in dry land was a foot greater than in 1922, while growth in the irrigated plots was much the same as before. The respective heights in dry land, partially and fully irrigated plots were 15, 41, and 43 inches and the yields 3, 32, and 29 bushels. The roots of corn made the best development in the lightly irrigated plot, and this was correlated with the best yield of 125 bushels per acre, the yield being 25 bushels for dry land and 115 for full irrigation.

CUT-QUADRAT PHYTOMETERS.

The growth of a representative area of a community may be used as a climatic index as well as a measure of response in much the same way as transpiration. It possesses three distinct advantages over the latter, though the two are complementary and hence one can not replace the other. Growth demands no laborious installation, as it can be determined directly from the native or culture community in position. While it can be measured at

any time, it yields the major values at the end of the growing-season, and thus does not require the services of a resident investigator. Moreover, it integrates the response for the whole season, though as a complex it permits less ready analysis than transpiration and is also less satisfactory for short periods. In short, it is the simplest and most convenient of all community phytometers when employed in the form of the cut or clip quadrat. This is the only practicable method, as the measurement of the individuals in a community group is too time-consuming to be desirable. There are certain cases in which it is profitable to pull the individuals out with their roots, but this is hardly feasible in a close cover or a compact soil. The clip-quadrat is merely the usual one of a square meter in extent, from which the shoots are cut at any desired time. It may be either smaller or larger in order to meet special conditions, as in the case of crops planted in rows. The growth is regularly expressed in terms of dry matter, but in the case of grazing ranges or forage crops, the green weight should likewise be found. Finally, the clip-quadrat facilitates the analysis of community response to climatic factors by making it possible to measure growth during different portions of the season or its variations from season to season or from the wet to the dry phase of a climatic cycle, and to determine the part played by the various species in the total production.

In the case of the grains, it is often preferable to select the individuals to be cut in accordance with the results desired, instead of taking all those in a particular area (Weaver, Jean, and Crist, 1922). This may be regarded as an aggregate clip-quadrat; it has the further advantage of permitting measurement of particular individuals throughout the season.

Clip-quadrats were first installed at the three stations in 1920; these represented high and low prairie in the true-prairie association, mixed prairie, and short-grass plains (Weaver, 1924). They were again cut in 1921 and 1922 to determine the fluctuation from year to year. The first step in the simple procedure was to select a considerable number of quadrats in typical areas of each climax. The height and density of the cover, the abundance of dominant and subdominant species, the presence of layers, etc., were recorded and photographs made of certain of the quadrats. In some instances it has proved desirable to make a chart of these as well. The cover was then removed by cutting it near the surface and at a uniform level with a hand-clipper. It was collected, sorted, and then shipped into the laboratory to be thoroughly air-dried, after which the actual production was determined on the basis of the dry weight. This gave an expression of the growth of the community as a unit, as well as the rôle taken by each dominant or subdominant in this. As complete factor records were obtained at each station, this made it possible to correlate the yield of community or species with the climate and the season at each (plate 10B).

Since even the most uniform cover shows some variation in density, the clip-quadrats were selected with much care and in sufficient number to insure dependable results. As in all ecological studies that are adequate, i. e., causal and quantitative rather than merely mathematical, this demands considerable knowledge of the community and can not be met by random selection. The best plan is to locate a proper proportion of quadrats in

pure or nearly pure stands of each dominant whenever these are present and to distribute the others among the various mixtures. It is often desirable to take the subdominants into account in doing this, as their yield may be much greater than that of the grasses.

Results at Grassland Stations.

In every case each grass or mixture of grasses yielded progressively less as the rainfall and holard decreased to the westward. The only exception is the case of buffalo-grass at Lincoln in 1921, and this is readily explained

Table 6.—*Average yield of clip-quadrats, in grams.*

Dominant type of vegetation.	1920.			1921.			1922.		
	Lincoln.	Phillipsburg.	Burlington.	Lincoln.	Phillipsburg.	Burlington.	Lincoln.	Phillipsburg.	Burlington.
Buffalo-grass	.....	290	98	235	266	207	.....	260	179
Wheat-grass	.....	541	500	606	457	400	541	334	.....
Mixed short and tall grasses	.....	313	197	.....	.....	.....	.....	365	263
Mixed tall-grasses	458	410	.....	755	477	.....	413	287	.....
Average, based on number of quadrats	458	378	183	603	402	353	447	311	224

as an effect of grazing. Moreover, the averages for each year at the several stations show a graduated series, plant production increasing with increased efficiency of rainfall. However, it may be readily seen that the total yield at all of the stations was greater in 1921 than during the preceding or following year, an increase particularly noticeable in the case of the late-maturing tall-grasses (table 6).

There was a pronounced decrease in the height of all three species from Lincoln westward, the plants at Burlington averaging less than half as tall as at Lincoln. With respect to weight, the differences were even greater, oats and wheat yielding a third as much as at Lincoln. The average production for the three crops was 2,234 at Lincoln, 1,164 at Phillipsburg, and 882 at Burlington, in close correspondence with rainfall, evaporation, and chresard (table 7).

Results in Grazing Exclosures.

Experimental exclosures were installed in three representative areas of northern Arizona in 1918 in cooperation with the Biological Survey of the United States Department of Agriculture (Taylor and Loftfield, 1922, 1923). While these were designed to serve several purposes, the most important was to evaluate the rôle of grazing in the structure and yield of grassland and to determine the effect of the food-habits of the prairie-dog of the region (*Cynomys gunnisoni zuniensis*) upon the carrying capacity and composition of the range. The latter is a portion of the mixed-prairie association, usually modified in this region by the suppression of the tall-

grasses through overgrazing. The northern area lies in Coconino Wash, about 9 miles south of the Grand Canyon, and consists of *Agropyrum glaucum* and *Sporobolus cryptandrus*, with small amounts of *Bouteloua gracilis*, *Stipa comata*, and other grasses. The exclosure consists of two equal parts, proof against both cattle and rodents, but with one containing a group of prairie-dogs, and it lies beside an unfenced area provided with quadrats also. This series has permitted a quantitative study of the vegetation under three conditions: (1) under total protection, (2) grazed by

TABLE 7.—*Growth and yield of crop-quadrats, 1923.*

Crop and station.	Date of harvest.	Height.	Weight.
		in.	*gm.*
Oats:			
Lincoln	July 7	42	2,637.0
Phillipsburg	July 3	32	905.0
Burlington	July 7	18	806.5
Wheat:			
Lincoln	July 7	42	2,395.0
Phillipsburg	July 3	29	1,296.0
Burlington	July 7	24	801.5
Barley:			
Lincoln	July 2	43	1,671.5
Phillipsburg	July 3	37	1,292.5
Burlington	July 7	26	1,038.5

cattle alone, and (3) grazed by a known number of prairie-dogs. Similar exclosures are located at Williams and at Seligman, the former in a community of *Bouteloua gracilis* and *Muhlenbergia gracillima*, the latter in one of *B. gracilis* and *eriopoda*.

TABLE 8.

	Agropyrum glaucum.			Sporobolus cryptandrus.			Total quantity of grass.		
	1919.	1920.	1921.	1919.	1920.	1921.	1919.	1920.	1921.
Total protection	100.0	117.1	138.8	164.6	32.8	81.9	264.6	149.9	220.7
Rodent grazing	36.8	24.3	22.6	Trace.	None.	None.	36.8	24.3	22.6
Cattle and rodent grazing	6.6	8.7	6.7	4.6	None.	6.4	11.2	8.7	13.1

The growth of the grasses under the three conditions has been measured by means of clip-quadrats, and at the Coconino station has yielded the figures presented in table 8, expressed as grams of forage per square meter:

Agropyrum glaucum shows a consistent increase for the three years of total protection, probably owing to its better utilization of rainfall as a result of its sod habit (plate 11A). As a bunch-grass, *Sporobolus cryptandrus* appears to be more dependent upon the seasonal distribution of the rainfall, and it is also unable to hold its own in competition with the increasing *Agropyrum*. Rodents are especially fond of it, as are cattle also; but while the latter merely graze it to the ground, the prairie-dogs destroy it completely by the second year.

TRANSPLANT PHYTOMETERS.

Species Phytometers.

As the basic method in the ecological organization of the field of experimental evolution (Clements and Hall, 1918–1923; Clements and Clements, 1923) and in the development of the new field of experimental vegetation (Clements and Weaver, 1918–1923, 1924), transplant gardens and areas have been installed in a number of climatic and edaphic series in the West. The climatic transect in the grassland extends from Nebraska City in the subclimax prairie with a rainfall of 33 inches, to Lincoln in the true prairie with 28 inches, Phillipsburg in mixed prairie with 23 inches, and Burlington and Colorado Springs in varying types of mixed prairie and short-grass plains with a rainfall of 17 and 15 inches respectively. The edaphic transect at Lincoln runs through swamp, salt-flat, low prairie, high prairie, and gravel-knoll in the true-prairie climax and climate. The Petran transect at Pike's Peak extends from mixed prairie with a 15-inch rainfall at Colorado Springs through successive zones of montane, subalpine, and alpine climaxes to a rainfall of 30 inches on the summit of the Peak, while the Sierran transect reaches from the Pacific Ocean to the summit of the Sierra Nevada and the sagebrush desert of the Great Basin. Edaphic transects have also been installed in various climates in these two major climatic series, but have been especially developed at the Alpine Laboratory and at Mather in the Hetch-Hetchy Valley. In addition to these, adaptation or ecad sequences of flowering plants have been developed in varying amounts of water-content or light, and similar sequences have been established for fungi and lichens, mosses, etc.

Practically all transplant installations have been designed to serve a dual purpose, namely, plant response and factor measurement. In the mountain transects, evolution has so far been the primary objective and habitat analysis the secondary, while in the grassland series measurement of climate and climax has been paramount and adaptation secondary. However, both have been constantly kept in mind as reciprocals in the complete synthesis of plant and habitat. While these are an intrinsic part of the comprehensive phytometer method, the detailed account is necessarily left for the respective treatments (cf. Clements and Weaver, 1924).

Community Phytometers.

The development of community transplants as phytometers has necessarily been slower, because of the difficulties involved, especially those of transportation. These are most readily solved in the case of sod-cores or blocks, but the latter are too small for many of the phytometric values sought. In the case of exclosures and inclosures, community phytometers of practically any desired size are possible, but these are limited to measurements of the effect of grazing or other animals (plate 11B). A further type of community phytometer with essentially the value of transplanting is obtained by modifying the holard through irrigating, flooding, or draining, or changing the light intensity by thinning, clearing, or producing an artificial canopy or shade. In practice, however, community phytometers have been confined largely to grassland and to lichens and mosses. In the

case of the latter, entire communities are moved with the greatest readiness, but with sod or turf only fragments can be transported as a rule. The most feasible method of doing this is to cut a meter quadrat into four parts, which are then readily moved if the soil-blocks are not too thick. Areas several meters square have been transferred in this way from the alpine meadow to the montane climax. The simplest and most successful device for transplanting a community has been that of the reciprocal transplant quadrat, in which the central portions of two permanent quadrats are interchanged (Clements and Loftfield, 1923).

In addition to the experimental transfers employed as phytometers are the large number of natural communities of definite limits, which occur as pioneers or relicts. These have the advantage of requiring no installation, but they are correspondingly less amenable to control. Their utilization as definite experiments under instrumental conditions has just been begun and the range of their usefulness is yet to be determined.

RÉSUMÉ.

Values and Limitations of the Phytometer Method.

The six years of experience with the phytometer method in a wide variety of forms and applications seem to justify the conclusion that it is indispensable to all quantitative studies. Its sole limitation is the labor and expense involved, and this applies only to growth phytometers carried out on a large scale for the entire season. Even with these, when growth is expressed in yield or dry weight for the whole season, the operation is within the capacity of a single investigator, and this is still truer of short-period phytometers utilizing a simple function, such as transpiration. Moreover, it is an advantage rather than a limitation that phytometric studies must be carried through several seasons to obtain representative results, in so far as climate is concerned, a fact that applies with equal force to instrumental measurements as well. This is true also of edaphic applications, since local habitats vary with the seasonal swing. In spite of this, installations of phytometers for a single season have a wide range of usefulness whenever comparative values are sought independently of the annual variations. While the best use of phytometers is in conjunction with instruments, they render recording instruments necessary only in the more extensive installations. In fact, it is to be expected that the increasing standardization of phytometers will cause them to largely replace the less satisfactory instruments, such as the atmometer in its various forms.

It seems unnecessary to recapitulate the many uses of the various kinds of phytometers, but it is desirable to emphasize the leading rôle played by the phytometer in the exact analysis of the processes and changes of vegetation and crops. The plant or community alone can measure the factor-complex, as well as the efficient factors in it and the effect of their annual fluctuation. They are the only measures of the decisive part played by competition, and of the far-reaching effect of animal reactions upon vegetation. Finally, it is only by the exact evaluation of the control exerted by factor, competition, and animals that it becomes possible to distinguish present and past effects in vegetation.

TABLES.

TABLE 9.—*Results from sealed phytometers, 1918.*

FIRST SERIES.

Station.	Species.	No. stalks.	Total water used.	Dry weight.	Water requirement.	Ave. water requirement.	Rel. water requirement.	Leaf area, sq. dm.	Transpiration per sq. dm.	Ave. transpiration per sq. dm.	Rel. transpiration per sq. dm.	Relative dry weight.
			gm.	*gm.*	*gm.*	*gm.*			*gm.*	*gm.*		
Plains	Sunflower	1	932	1.673	557	....	....	2.35	396.6	....	....	....
Do	Do	1	962	1.930	498	....	....	2.65	363	....	....	....
Do	Do	1	1,022	2.185	468	518	100	2.89	353.6	376	100	100
Do	Do	1	1,066.5	1.947	548	....	....	2.73	390.7	....	....	....
Montane	Do	1	497	1.324	375	....	....	2.31	215.2	....	....	....
Do	Do	1	808.6	2.103	384	....	....	2.89	279.8	....	....	....
Do	Do	1	820	2.234	367	370	71	2.89	283.7	264.3	70	101
Do	Do	1	714.8	1.966	364	....	....	2.74	260.9	....	....	....
Do	Do	1	764	2.132	358	....	....	2.71	281.9	....	....	....
Plains	Beans	6	3,033	5.593	542	542	100	7.43	408.2	408.2	100	100
Montane	Do	6	2,109	5.776	365	365	67	8.84	238.6	238.6	58	103
Plains	Oats	6	384	.530	725	765	100	....	....	....	....	100
Do	Do	4	367	.452	812	....	....	....	....	....	....	....
Montane	Do	8	218	.456	478	....	....	....	....	....	....	....
Do	Do	4	104	.225	462	....	....	....	....	....	....	65
Do	Do	6	177	.286	619	509	66	....	....	....	....	....
Do	Do	6	281.5	.515	547	....	....	....	....	....	....	....
Do	Do	4	130.5	.296	441	....	....	....	....	....	....	....
Plains	Wheat	5	295	.385	766	766	100	....	....	....	....	100
Montane	Do	4	210.7	.276	763	....	....	....	....	....	....	91
Do	Do	10	384.5	.699	550	657	86	....	....	....	....	....

SECOND SERIES.

			gm.	*gm.*	*gm.*	*gm.*			*gm.*	*gm.*		
Plains	Sunflower	1	4,124	10.873	379	382	100	7.70	535.6	507.8	100	100
Do	Do	1	4,018	10.439	384	....	....	8.37	480	....	....	....
Montane	Do	1	2,468.5	8.273	298	285	74	9.90	249.3	251.9	50	....
Do	Do	1	2,432	8.988	271	....	....	9.56	254.4	....	....	81
Plains	Oats	20	1,677	3.533	475	536	100	5.85	286.7	367.3	100	100
Do	Do	13	1,012	1.699	596	....	....	2.26	447.8	....	....	....
Montane	Do	27	1,512.5	5.283	286	335	63	10.69	141.5	162	44	....
Do	Do	26	1,312	3.417	384	....	....	7.19	182.5	....	....	166
Plains	Wheat	9	1,014	1.753	578	486	100	1.95	520	386	100	100
Do	Do	14	784	1.900	394	....	....	2.97	251.9	....	....	....
Montane	Do	23	1,537.5	4.672	329	320	66	7.25	212.1	197.2	51	....
Do	Do	20	1,190.5	3.842	310	....	....	6.53	182.3	....	....	230
Plains	Sweet clover.	5	510.5	.965	529	529	100	....	....	....	....	100
Montane	Do	4	130.5	.511	255	....	....	....	....	....	....	....
Do	Do	5	175	.590	297	300	57	....	....	....	....	....
Do	Do	3	239	.684	349	....	....	....	....	....	....	62

TABLE 9.—*Results from sealed phytometers, 1918*—Continued.

THIRD SERIES.

Station.	Species.	No. stalks.	Total water used.	Dry weight.	Water requirement.	Ave. water requirement.	Rel. water requirement.	Leaf-area, sq. dm.	Transpiration per sq. dm.	Ave. transpiration per sq. dm.	Rel. transpiration per sq. dm.	Relative dry weight.
			gm.	*gm.*	*gm.*	*gm.*			*gm.*	*gm.*		
Plains	Sunflower	1	1,873	1.734	1,080	.....	....	1.98	946	.....	.....	.....
Do	Do	1	1,869	1.557	1,200	1,140	100	1.88	994.1	970.1	100	100
Montane	Do	1	935.5	2.654	352	.....	....	3.16	296	.....	.....	....
Do	Do	1	954.2	3.037	314	.....	....	3.07	310.8	.....	.....	....
Do	Do	1	811.2	1.806	449	372	33	2.52	321.9	309.6	32	152
Gravel-slide	Do	1	709	1.496	474	.....	....	2.64	268.6	.....	.....	....
Do	Do	1	1,170	2.393	489	.....	....	3.35	349.3	.....	.....	....
Do	Do	1	978	1.945	503	489	43	2.84	344.4	320.8	33	118
Douglas fir	Do	1	74	.306	242	.....	....	.62	119.4	.....	.....	....
Do	Do	1	110	.318	346	.....	....	.74	148.6	.....	.....	....
Do	Do	1	115	.307	375	321	28	.73	157.5	141.8	15	19
Spruce	Do	1	164	.419	391	.....	....	.72	227.8	.....	.....	....
Do	Do	1	74.5	.309	241	316	27	.67	111.2	169.5	17	22
Plains	Oats	6	885	.953	929	.....	....	1.57	563.7	.....	.....	....
Do	Do	6	1,174	1.370	857	893	100	2.57	456.8	510.3	100	100
Montane	Do	6	501.1	.840	597	.....	....	1.31	382.5	.....	.....	....
Do	Do	6	500.2	1.057	473	535	60	1.74	287.5	335	66	82
Gravel-slide	Do	5	412.5	.843	489	.....	....	1.24	332.7	.....	.....	....
Do	Do	4	360.5	.527	684	.....	....	1.01	356.9	.....	.....	....
Do	Do	4	431.2	.781	552	575	64	.9	479.1	389.6	76	62
Douglas fir	Do	3	20.2	.102	198	.....	....	.16	33.6	.....	.....	....
Do	Do	4	23	.203	113	156	17	1.00	23	28.3	6	13
Spruce	Do	4	85	.271	314	.....	....	1.24	68.5	.....	.....	....
Do	Do	3	60.4	.185	326	320	36	.87	69.4	69	14	20
Plains	Rubus	1	721	.....	.....	.....	....	1.91	377.5	.....	.....	....
Do	Do	1	856.5	.....	.....	.....	....	1.78	481.2	.....	.....	....
Do	Do	1	863.5	.....	.....	.....	....	2.51	344	400.9	100	....
Montane	Do	1	252.5	.....	.....	.....	....	1.09	231.7	.....	.....	....
Do	Do	1	295.8	.....	.....	.....	....	1.18	250.7	.....	.....	....
Do	Do	1	152.5	.....	.....	.....	....	.73	208.9	230.4	57	....
Gravel-slide	Do	1	318	.....	.....	.....	....	1.29	246.5	.....	.....	....
Do	Do	1	259.5	.....	.....	.....	....	.75	346	.....	.....	....
Do	Do	1	83	.....	.....	.....	....	.54	153.7	248.7	62	....
Douglas fir	Do	1	33	.....	.....	.....	....	.80	41.3	.....	.....	....
Do	Do	1	96.5	.....	.....	.....	....	1.02	94.6	.....	.....	....
Do	Do	1	45	.....	.....	.....	....	.77	58.4	64.8	16	....
Spruce	Do	1	46	.....	.....	.....	....	.42	109.5	.....	.....	....
Do	Do	1	63.7	.....	.....	.....	....	.69	92.3	.....	.....	....
Do	Do	1	50.5	.....	.....	.....	....	.56	90.2	97.3	24	....

TABLE 10.—*Summary of sealed phytometers, 1918.*

Station.	Species.	Series.	No. pots.	No. stalks	Ave. dry weight	Ave. water requirement.	Rel. water requirement.	Ave. leaf-area	Ave. transpiration per sq. dm.	Rel. transpiration per sq. dm.	Period.	No. days
					gm.	*gm.*		*sq. dm.*	*gm.*			
Plains	Sunflower	1	4	4	1.934	518	100	2.66	376	100	June 13 to July 10	27
Montane	Do	1	5	5	1.952	370	71	2.71	264	70	June 14 to July 10	26
Plains	Do	2	2	2	10.656	382	100	8.02	508	100	June 14 to July 22	45
Montane	Do	2	2	2	8.631	285	74	9.73	252	50	Do	45
Plains	Do	3	2	2	1.646	1,140	100	1.93	970	100	July 10 to Aug. 16	37
Montane	Do	3	3	3	2.499	372	33	2.92	310	32	Do	37
Gravel-slide	Do	3	3	3	1.945	489	43	2.94	321	33	Do	37
Douglas fir	Do	3	3	3	.310	322	28	.70	142	15	Do	37
Spruce	Do	3	2	2	.364	316	28	.70	170	17	Do	37
Plains	Beans	1	6	6	.932	542	100	1.24	408	100	June 17 to July 10	23
Montane	Do	1	6	6	.963	365	67	1.47	239	58	Do	23
Plains	Oats	1	2	10	.098	765	100	.....	.....	.....	Do	.....
Montane	Do	1	5	28	.064	509	66	.....	.....	.....	Do	.....
Plains	Do	2	2	33	.159	536	100	.25	367	100	June 15 to July 22	37
Montane	Do	2	2	53	.164	335	63	.34	162	44	Do	37
Plains	Do	3	2	12	.194	893	100	.35	510	100	July 10 to Aug. 16	37
Montane	Do	3	2	12	.158	535	60	.25	335	66	Do	37
Gravel-slide	Do	3	3	13	.165	575	64	.24	390	76	Do	37
Douglas fir	Do	3	2	7	.044	156	17	.17	28	6	Do	37
Spruce	Do	3	2	7	.065	320	36	.30	69	14	Do	37
Plains	Wheat	1	1	5	.077	766	100	.....	.....	.....	June 15 to July 10	25
Montane	Do	1	2	14	.070	657	86	.....	.....	.....	Do	25
Plains	Do	2	2	23	.159	486	100	.21	386	100	June 15 to July 22	37
Montane	Do	2	2	43	.198	320	66	.32	197	51	Do	37
Plains	Sweet clover	2	1	5	.193	529	100	.....	.....	.....	June 7 to July 22	45
Montane	Do	2	3	12	.149	300	57	.....	.....	.....	Do	45
Plains	Rubus	3	3	3	.....	.....	.....	2.07	401	100	July 15 to Aug. 16	32
Montane	Do	3	3	3	.....	.....	.....	1.00	230	57	Do	32
Gravel-slide	Do	3	3	3	.....	.....	.....	.86	249	62	Do	32
Douglas fir	Do	.....	.....	.....	.....	.....	.....	.86	65	16	Do	32
Spruce	Do	3	3	3	.....	.....	.....	.56	97	24	Do	32

TABLE 11.—*Results from unsealed phytometers, 1918.*

SECOND SERIES.

Station.	Species.	No. of pots.	No. of plants.	Leaf-area.	Dry weight.	Ave. leaf-area.	Ave. dry weight.	Rel. dry weight.
				sq. dm.		*sq. dm.*	*gm.*	
Plains	Sunflower	3	3	6.25	7.573	2.08	2.524	.....
Montane	Do	2	2	5.51	5.674	2.76	2.837	81
Plains	Beans	5	5	9.29	4.898	1.86	.98	.....
Montane	Do	4	4	4.27	2.455	1.07	.61	62
Plains	Oats	5	48	.....	7.477	.....	.156	.....
Montane	Do	6	40	.....	5.468	.....	.137	88
Plains	Wheat	3	44	.....	9.361	.....	.213	.....
Montane	Do	3	36	.....	4.134	.....	.115	54

THIRD SERIES.

				sq. dm.		*sq. dm.*	*gm.*	
Plains	Sunflower	5	5	12.09	9.274	2.42	1.855	100
Montane	Do	5	5	12.29	8.610	2.46	1.722	93
Gravel-slide	Do	5	5	6.87	4.440	1.37	.888	48
Douglas fir	Do	2	2	1.29	.240	.65	.120	7
Spruce	Do	3	3	.86	.475	.29	.158	9
Plains	Oats	5	93	.....	9.277	.....	.100	100
Montane	Do	5	82	.....	10.806	.....	.132	132
Gravel-slide	Do	5	74	.....	8.690	.....	.117	117
Douglas fir	Do	5	90	.....	3.742	.....	.042	42
Spruce	Do	5	79	.....	4.364	.....	.055	55

TABLE 12.—*Summary of unsealed phytometers, 1918.*

Station.	Species.	Series.	No. of pots.	No. of stalks.	Ave. dry weight.	Ave. leaf-area.	Period.	No. days.
					gm.	*sq. dm.*		
Plains	Sunflower	2	3	3	2.524	2.08	June 12 to July 22	40
Montane	Do	2	2	2	2.837	2.76	Do	40
Plains	Do	3	5	5	1.855	2.42	July 10 to Aug. 16	35
Montane	Do	3	5	5	1.722	2.46	Do	35
Gravel-slide	Do	3	5	5	.888	1.37	Do	35
Douglas fir	Do	3	2	2	.120	.65	Do	35
Spruce	Do	3	3	3	.158	.29	Do	35
Plains	Oats	2	5	48	.556	.....	June 24 to July 22	28
Montane	Do	2	6	40	.137	.....	Do	28
Plains	Do	3	5	93	.100	.....	July 10 to Aug. 16	35
Montane	Do	3	5	82	.132	.....	Do	35
Gravel-slide	Do	3	5	74	.117	.....	Do	35
Douglas fir	Do	3	5	90	.042	.....	Do	35
Spruce	Do	3	5	79	.055	.....	Do	35
Plains	Beans	2	5	5	.980	1.86	June 24 to July 22	28
Montane	Do	2	4	4	.610	1.07	Do	28
Plains	Wheat	2	3	44	.213	.....	Do	28
Montane	Do	2	3	36	.115	.....	Do	28

TABLE 13.—*Results from sealed phytometers, 1919.*

FIRST SERIES.

Station.	Species.	No. of pots.	Ave. dry weight per plant.	Ave. water requirement.	Rel. water requirement.	Ave. leaf-area.	Ave. transpiration per sq. dm.	Rel. transpiration per sq. dm.	Period.	Days.
			gm.	*gm.*		*sq.dm.*	*gm.*			
Plains....	Sunflower	5	12.653	401	100	7.883	644	100	June 24 to Aug. 1	38
Do...	Wheat...	5	1.606	557	100	2.146	384	100	....Do.....	38
Do...	Oats.....	3	1.252	567	100	2.008	354	100	....Do.....	38
Do...	Beans....	5	5.803	665	100	8.977	430	100	June 26 to Aug. 1	36
Montane.	Sunflower	5	6.444	352	87	5.330	420	65	June 27 to Aug. 1	35
Do...	Wheat...	5	2.573	351	68	3.981	226	58	June 24 to Aug. 1	38
Do...	Oats.....	5	1.724	342	59	3.660	158	44	....Do.....	38
Do...	Beans....	5	2.623	424	63	4.429	251	58	June 26 to Aug. 1	36
Subalpine	Sunflower	5	2.967	280	72	3.741	230	35	June 25 to Aug. 1	37
Do...	Wheat...	3	1.764	173	26	3.07	78	20	....Do.....	37
Do...	Oats.....	3	1.632	249	43	3.041	133	37	....Do.....	37
Do...	Beans....	4	.822	287	47	1.061	245	56	....Do.....	37
					SECOND SERIES.					
			gm.	*gm.*		*sq.dm.*	*gm.*			
Plains....	Sunflower	2	5.806	669	100	4.724	822	100	Aug. 5 to Sept. 8	34
Do...	Wheat...	2	.482	977	100	1.023	460	100	Aug. 14 to Sept. 8	25
Do...	....Do...	2	1.128	858	100	3.517	218	100	Aug. 5 to Sept. 8	34
Do...	Oats.....	3	1.739	778	100	3.538	382	100	Aug. 7 to Sept. 8	32
Montane.	Sunflower	3	2.107	592	88	2.207	565	69	Aug. 6 to Sept. 8	33
Do...	Wheat...	3	.116	931	95	.240	450	98	....Do.....	33
Do...	....Do...	2	.542	644	75	.893	390	179	....Do.....	33
Do...	Oats.....	3	1.463	1,075	138	3.480	452	118	Aug. 8 to Sept. 8	31
Subalpine	Sunflower	3	2.177	513	77	2.762	404	49	Aug. 4 to Sept. 8	35
Do...	Wheat...	3	.628	622	63	1.091	358	77	....Do.....	35
Do...	....Do...	2	1.293	594	69	2.331	329	150	Aug. 11 to Sept. 8	28
Do...	Oats.....	3	.692	609	78	1.359	310	81	Aug. 9 to Sept. 8	36

TABLE 14.—*Results from sealed phytometers, 1920.*

Station.	First series.				Second series.		
	Species.	Aver. total transpiration.	Aver. dry weight.	Aver. water requirement.	Aver. total transpiration.	Aver. dry weight	Aver. water requirement.
		gm.	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
Plains.....	Sunflower....	1,734	3.8045	456.30	2,967	6.7879	437.10
Montane....	....Do.....	1,311	3.1582	415.07	5,180	14.5083	357.04
Subalpine...	....Do.....	359	.829	434.29	1,465.9	3.7213	396.60
Plains.....	Wheat.....	1,050	1.604	650.99	145.2	.3151	460.8
Montane....	....Do.....	740	1.3943	530.70	1,108.7	2.5341	437.51
Subalpine...	....Do.....	408	.7541	543.35	703.4	2.0122	349.56
Plains.....	Oats.....	1,529	2.7186	543.35	2,356.6	5.4923	429.07
Montane....	....Do.....	965	1.8082	532.41	1,759.5	4.3182	407.46
Subalpine...	....Do.....	497	.954	520.96	566.8	1.2892	133.74

TABLE 15.—*Average stem length and width of sunflowers in millimeters, 1920.*

FIRST SERIES.

Station.	June 14 to 21.	June 21 to 28.	June 28 to July 5.	July 5 to 12.	July 12 to 19.
Plains	42.6	63.8	123.2	191	285.4
Montane	16.4	32.2	74.4	132	212
Subalpine	14	14.8	42.6	62.8	93
Plains	2.88	3.12	4.26	5.54	6.80
Montane	2.42	2.50	3.68	5.56	7.20
Subalpine	2.55	2.57	3.34	4.18	5.40

SECOND SERIES.

Station.	July 19 to 26.	July 26 to Aug 2.	Aug. 2 to 9.	Aug. 9 to 16.	Aug. 16 to 23.	Aug. 23 to 30.
Plains	16.8	38.8	57.2	87.2	166.8	287.4
Montane	17.6	31.6	67.6	115.4	171.8	243.6
Subalpine	17.6	20.6	35.4	58	75.2	107.6
Plains	1.76	2.04	2.72	3.2	4.14	4.94
Montane	2.24	2.50	3.42	4.62	5.82	7.04
Subalpine	2.46	2.38	2.74	3.52	4.12	5.02

TABLE 16.—*Average daily transpiration of sunflower phytometers, 1923.*

FIRST SERIES.

	June 13 to 18.	June 18 to 25.	June 25 to July 1.	July 1 to 3.	July 3 to 5.	July 5 to 7.	July 7 to 9.	July 9 to 12.	July 12 to 14.
Sun Station:									
Average daily water-loss (c. c.)	16.2	32.37	32.48	31.00	67.50	85.00	90.00	47.90	85.90
Average leaf-area (sq. dm.)	0.627	0.871	1.511	1.908	2.342	2.777	2.994	3.628	3.959
Transpiration per sq. dm.	25.8	37.16	21.49	16.24	28.82	30.60	30.06	13.20	21.69
Half-shade station:									
Average daily water-loss (c. c.)	8.2	14.7	11.3	21.0	23.8	33.0	44.0	36.2	42.6
Average leaf-area (sq. dm.)	0.835	1.026	1.497	1.778	2.092	2.395	2.604	2.872	3.088
Transpiration per sq. dm.	9.81	14.32	7.54	11.86	11.37	15.77	16.89	12.60	13.79
Shade station:									
Average daily water loss (c. c.)	14.8	9.95	9.15	10.0	14.3	20.5	12.8	8.98	8.10
Average leaf-area (sq. dm.)	0.792	0.872	0.999	1.047	1.114	1.181	1.248	1.302	1.327
Transpiration per sq. dm.	20.87	11.39	9.15	9.55	12.83	17.36	10.26	6.89	6.10

SECOND SERIES.

	Aug. 2 to 6.	Aug. 6 to 13.	Aug. 13 to 20.	Aug. 20 to 27.	Aug. 27 to Sept. 3.
Sun station:					
Average daily water-loss (c. c.)	3.97	3.60	2.58	6.20	4.96
Average leaf-area (sq. dm.)	34.22	42.17	55.92	65.56	78.05
Transpiration per sq. dm.	11.60	8.53	4.61	9.45	6.11
Half-shade station:					
Average daily water-loss (c. c.)	1.60	3.00	1.50	2.80	1.32
Average leaf-area (sq. dm.)	35.24	41.04	51.84	53.99	49.72
Transpiration per sq. dm.	4.54	7.30	2.89	5.18	2.65
Shade station:					
Average daily water-loss (c. c.)	0.47	0.91	0.50	0.53	0.40
Average leaf-area (sq. dm.)	31.64	36.94	44.96	50.82	51.68
Transpiration per sq. dm.	1.48	2.47	1.11	1.04	0.77

TABLE 17.—*Growth of sunflower phytometers, 1923.*

FIRST SERIES.

Date.	Sun station.		Half-shade station.		Shade station.	
	Phytometers.	Checks.	Phytometers.	Checks.	Phytometers.	Checks.
Average leaf-area in sq. cm.:						
June 18	62.70	.....	83.56	.....	79.20	.....
June 25	111.55	100.68	121.71	104.08	95.22	77.87
July 2	190.82	174.26	177.82	134.06	104.71	81.28
July 9	342.99	.....	274.20	.....	128.25	.....
July 13	395.90	492.41	308.88	169.24	135.20	96.26
Average stem-length in mm.:						
June 18	48.2	.....	72.9	.....	84	.....
June 25	82.7	119	165.2	178	181.5	187
July 2	116	136	264.6	230	244.7	228
July 9	180.5	.....	393	.....	338.1	.....
July 13	203.3	226	428.2	330	304.8	238
Average stem-diameter in mm.:						
June 18	4	.....	3.80	.....	3.70	.....
June 25	3.90	4.30	4.20	4	3.65	3.70
July 2	5.47	4.60	5.24	4.30	3.91	3.71
July 9	6.54	.....	6.09	.....	4.02	.....
July 13	7.45	6	6.64	4.40	4.27	3.70
SECOND SERIES.						
Average leaf-area in sq. cm.:						
Aug. 6	34.22	38.05	35.24	40.19	31.64	31.37
Aug. 13	50.13	46.82	46.84	51.79	42.24	38.86
Aug. 20	61.72	55.51	56.85	63.03	47.69	45.72
Aug. 27	69.40	69.08	51.13	67.28	53.95	50.09
Sept. 3	86.71	96.90	48.32	75.09	59.41	54.43
Average stem-length in mm.:						
Aug. 6	88.9	112.8	97.8	128.2	110.2	118.3
Aug. 13	105.5	130.5	125.5	165.5	156	160.5
Aug. 20	117.5	146.2	145	203.5	180	195
Aug. 27	145.5	137	162.1	234	200.6	214
Sept. 3	155.5	183.5	169.2	250.5	213.7	257
Average stem-diameter in mm.:						
Aug. 6	2.73	3.09	2.76	3.09	2.70	2.84
Aug. 13	3.15	3.34	3.20	3.29	2.70	2.87
Aug. 20	3.31	3.30	3.42	3.28	2.71	2.80
Aug. 27	3.51	3.54	3.80	3.28	2.68	2.86
Sept. 3	3.76	3.83	3.28	3.40	2.45	2.75

TABLE 18.—*Dry weight and water requirement of sunflower phytometers, 1923.*

FIRST SERIES.

Station.	Phytometers.				Checks.			Ave. water requirement.
	Leaves.	Stems.	Roots.	Plant.	Leaves.	Stems.	Shoot.	
Average dry weight in grams:								
Sun	1.2894	0.6393	0.4769	2.4056	0.8030	0.5500	1.353	804.9
Half-shade	.6233	.7750	.3352	1.7335	.3130	.4040	.7170	486.5
Shade	.1650	.1280	.0614	.3544	.1390	.1106	.2496	124.91

Station.	Leaves.	Stems.	Roots.	Leaves.	Stems.
Percentage of sun-station values:					
Sun	100	100	100	100	100
Half-shade	48.34	121.24	70.28	38.96	73.45
Shade	12.79	20.02	12.83	17.31	20.10

SECOND SERIES.

Station.	Phytometers.				Checks.			Ave. water requirement.
	Leaves.	Stems.	Roots.	Plant.	Leaves.	Stems.	Shoot.	
Ave. dry weight in grams:								
Sun	0.4589	0.3724	0.2047	1.0360	0.4792	0.3421	0.8213	165.1
Half-shade	.3402	.3694	.2789	.9885	.2142	.1553	.3695	94
Shade	.1695	.1412	.1024	.4131	.12778	.1293	.2571	58.7

Station.	Leaves.	Stems.	Roots.	Leaves.	Stems.
Percentage of sun-station values:					
Sun	100	100	100	100	100
Half-shade	74.1	99.2	135.2	44.6	45.3
Shade	36.9	37.9	50.0	26.6	37.7

TABLE 19.—*Individual variability in transpiration of sunflowers.*

FIRST SERIES.

(Disc. = Discarded)

No.	Loss in weight.	Ave. leaf product.	Loss per ave. product.	No.	Loss in weight.	Ave. lead product.	Loss per ave. leaf product.
	gm.		*gm.*		*gm.*		*gm.*
1	12.6	2,570	0.0049	51	13.1	2,609	0.0050
2	10.5	2,556	.0041	52	7.9	1,263	.0062
3	11.5	2,328	.0049	53	8.4	1,274	.0065
4	10.4	2,773	.0037	54	Disc.		
5	Disc.			55	13.5	2,877	.0046
6	14.7	2,575	.0057	56	Disc.		
7	Disc.			57	6.9	2,952	.0023
8	Disc.			58	Disc.		
9	21.8	3,451	.0063	59	11.7	2,430	.0047
10	Disc.			60	13.0	2,450	.0050
11	13.4	1,943	.0068	61	17.5	2,536	.0068
12	12.5	1,998	.0062	62	10.1	2,084	.0064
13	10.4	1,768	.0058	63	13.2	2,594	.0051
14	15.3	2,739	.0055	64	7.3	2,097	.0035
15	13.1	3,120	.0042	65	9.4	2,069	.0040
16	Disc.			66	14.0	2,916	.0048
17	Disc.			67	Disc.		
18	Disc.			68	10.5	1,867	.0058
19	19.5	1,899	.0050	69	Disc.		
20	Disc.			70	10.2	2,219	.0045
21	7.0	2,073	.0034	71	Disc.		
22	13.7	2,053	.0067	72	Disc.		
23	9.6	2,689	.0036	73	9.5	2,538	.0037
24	10 3	1,708	.0060	74	16.4	2,364	.0060
25	8.7	2,363	.0036	75	15.5	4,505	.0034
26	Disc.			76	16.9	3,636	.0048
27	10.8	2,474	.0044	77	15.0	3,109	.0048
28	18.0	3,010	.0061	78	10.4	3,088	.0034
29	Disc.			79	14.7	3,284	.0044
30	Disc.			80	10.4	2,993	.0031
31	14.3	2,495	.0056	81	14.6	3,313	.0044
32	15.0	2,527	.0059	82	8.1	3,137	.0026
33	10.1	2,469	.0041	83	9.8	2,834	.0035
34	16.4	2,599	.0063	84	14.7	3,604	.0041
35	11.1	2,036	.0055	85	7.5	2,609	.0029
36	7.6	2,188	.0035	86	15.5	3.254	.0051
37	4.8	2,292	.0021	87	Disc.		
38	5.0	2,315	.0021	88	5.6	1,886	.0027
39	Disc.			89	Disc.		
40	11.3	1,838	.0061	90	9.7	3,241	.0029
41	8.6	2,869	.0030	91	Disc.		
42	13.2	2,085	.0063	92	Disc.		
43	5.0	1,643	.0030	93	6.8	2,471	.0028
44	10.1	2,219	.0046	94	6.0	1,579	.0038
45	10.0	2,224	.0044	95	9.9	2,821	.0035
46	Disc.			96	9.7	1,932	.0050
47	9.6	1,490	.0064	97	Disc.		
48	9.4	1,679	.0056	98	17.1	3,513	.0049
49	11.8	2,200	.0053	99	20.7	3,762	.0055
50	7.7	1,887	.0040	100	Disc.		

TABLE 20.—*Individual variability in transpiration of sunflowers.*

SECOND SERIES.

No.	Loss.	Leaf-area (sq. cm.).	Loss per leaf-area.	No.	Loss.	Leaf-area (sq. cm.).	Loss per leaf-area.
	gm.		*gm.*		*gm.*		*gm.*
1	19.0	30.38	0.65	60	24.0	40.78	0.58
2	20.7	31.04	.66	61	17.6	24.26	.71
3	20.8	30.39	.68	62	15.9	29.61	.53
4	18.2	24.42	.74	63	Disc.		
5	19.6	33.24	.58	64	Disc.		
6	18.7	30.41	.61	65	Disc.		
7	15.7	28.75	.54	66	17.3	23.58	.73
8	17.0	31.08	.54	67	14.2	23.85	.59
9	33.7	52.16	.64	68	20.7	36.29	.54
10	19.0	40.84	.46	69	19.9	36.27	.52
11	16.4	27.99	.58	70	15.8	22.59	.69
12	12.4	26.03	.51	71	13.9	27.02	.51
13	15.6	30.74	.50	72	13.6	25.34	.53
14	18.3	42.42	.43	73	15.0	28.99	.51
15	Disc.			74	23.6	39.85	.59
16	6.9	33.50	.20	75	Disc.		
17	14.5	36.61	.31	76	10.8	16.05	.67
18	24.0	46.55	.52	77	14.8	23.77	.62
19	19.0	28.23	.67	78	14.2	26.92	.52
20	15.9	26.29	.60	79	14.7	22.11	.66
21	17.1	24.06	.71	80	17.3	34.28	.54
22	27.2	38.39	.71	81	Disc.		
23	15.9	26.58	.60	82	22.1	37.55	.59
24	14.0	26.29	.53	83	13.7	34.52	.39
25	23.5	33.69	.70	84	23.3	36.47	.63
26	14.5	23.59	.61	85	Disc.		
27	14.2	28.26	.50	86	20.0	39.12	.51
28	17.3	28.67	.60	87	14.9	29.46	.50
29	15.3	29.69	.51	88	21.1	23.85	.89
30	13.2	23.74	.55	89	11.3	21.46	.52
31	18.2	28.64	.63	90	16.3	28.98	.56
32	29.4	52.55	.55	91	20.6	17.95	.59
33	19.7	26.83	.73	92	Disc.		
34	27.1	61.02	.44	93	8.9	12.18	.73
35	11.0	24.87	.44	94	22.5	32.46	.69
36	17.1	29.04	.59	95	Disc.		
37	18.4	35.11	.52	96	21.5	36.33	.59
38	13.3	16.92	.74	97	21.6	41.72	.51
39	12.7	23.70	.53	98	16.0	27.12	.59
40	16.0	24.95	.64	99	16.2	25.10	.64
41	Disc.			100	17.9	23.35	.76
42	33.5	42.78	.77	101	20.0	31.44	.63
43	23.9	40.00	.59	102	Disc.		
44	17.4	39.20	.44	103	17.9	29.41	.60
45	Disc.			104	16.2	29.14	.55
46	17.9	33.09	.54	105	Disc.		
47	23.6	36.63	.64	106	Disc.		
48	Disc.			107	15.0	22.06	.67
49	14.7	23.05	.63	108	19.0	27.48	.69
50	15.8	24.25	.65	109	21.7	45.87	.49
51	10.3	17.61	.70	110	21.5	34.46	.62
52	17.2	28.38	.57	111	Disc.		
53	14.7	21.28	.69	112	18.9	30.35	.62
54	14.2	22.46	.63	113	19.0	26.13	.67
55	12.4	23.24	.53	114	Disc.		
56	13.7	25.12	.54	115	18.5	31.43	.58
57	10.7	22.24	.48	116	Disc.		
58	9.8	20.90	.46	117	18.6	32.61	.57
59	Disc.			118	14.7	22.76	.69

TABLE 21.—*Short-period phytometers, sun and shade, September 16, 1923.*

Sun.			Half-shade.			Shade.		
Loss in weight, 11 a. m. to 4 p. m.	Leaf product.	Loss per leaf product (raised to whole numbers).	Loss in weight, 11 a. m. to 4 p. m.	Leaf product.	Loss per leaf product (raised to whole numbers).	Loss in weight, 11 a. m. to 4 p. m.	Leaf product.	Loss per leaf product (raised to whole numbers).
gm.			*gm.*			*gm.*		
6.7	54,171	123	1.8	21,448	84	1.1	25,796	42
6.3	29,484	213	1.7	21,729	80	1.1	19,261	58
2.5	12,511	200	1.3	14,110	92	1.1	22,135	49
3.6	18,946	190	1.6	13,257	72	0.4	13,394	29

Average loss: Sun, 185; half-shade, 82; shade, 44.5; percentage of sun, 100, 44.3, 23.5.

TABLE 22.—*Short-period phytometers, sun and shade, September 18, 1923.*

Station.	Leaf product.	9 to 11 a. m.		11 a. m. to 1^h30^m p. m.		1^h30^m to 3 p. m.		3 to 5^h30^m p. m.	
		Loss.	Hourly loss per leaf product.	Loss.	Hourly loss per leaf product.	Loss.	Hourly loss per leaf product.	Loss.	Hourly loss per leaf product.
		gm.		*gm.*		*gm.*		*gm.*	
Sun	29,484	9.0	[1] 177	6.2	84	3.4	74	2.5	33
Do	54,171	8.2	75	9.2	67	4.3	52	2.4	17
Do	18,946	7.1	187	3.1	65	2.1	74	1.4	29
Do	12,511	5.4	211	2.6	83	2.1	111	.8	25
Half-shade	21,448	3.2	74	1.6	29	1.2	37	.3	55
Do	14,110	2.1	74	1.9	53	.5	23	.2	5
Do	11,814	1.2	50	1.7	57	.3	16	.2	6
Do	20,692	1.8	43	2.1	40	.8	25	.3	5
Shade	19,261	1.8	46	.9	18	.5	15	.1	2
Do	13,394	1.1	41	.6	17	.3	14	.1	2
Do	25,796	2.7	52	1.8	27	.7	18	.2	3
Do	21,729	2	46	1	18	.5	13	.2	3
Averages:									
Sun			167		75		78		26
Half-shade			60		45		25		18
Shade			46		20		15		25

Station.	Average hourly standard evaporation.				Temperature.				
	9 to 11 a. m.	11 a. m. to 1^h30^m p. m.	1^h30^m to 3 p. m.	3 to 5^h30^m p. m.	9 a. m.	11 a. m.	2 p. m.	3^h30^m p. m.	5^h30^m p. m.
	c. c.	*c. c.*	*c. c.*	*c. c.*	° *C.*	° *C.*	° *C.*	° *C.*	° *C.*
Sun	1.56	1.39	1.95	1.14	[2] 39.0	15.2	11.0	9.6	4.2
Half-shade	.71	.71	.83	.33	37.0	7.0	12.0	9.3	3.8
Shade	.70	.42	.46	.27	38.5	9.2	10.5	9.8	5.3

[1] Raised to whole numbers, as in all succeeding tables.

[2] The 9 a. m. readings were made at soil surface, all others at 3 inches above soil surface in shade.

TABLE 23.—*Short-period phytometers, surface and angle, September 20, 1923.*

Position.	Leaf product.	9 to 11 a. m.		11 a. m. to 1h30m p. m.		1h30m to 3h30m p. m.		3h30m to 4h30m p. m.	
		Loss.	Hourly loss per leaf product.	Loss.	Hourly loss per leaf product.	Loss.	Hourly loss per leaf product.	Loss.	Hourly loss per leaf product.
		gm.		*gm.*		*gm.*		*gm.*	
Level turf	14,110	3.7	131	6.5	184	3.4	120	0.6	28
Do	11,814	3.3	148	3.8	120	4.1	173	1.1	62
Do	20,692	5.1	120	6.8	131	6.1	247	2.4	77
Level gravel	12,969	3.3	127	3.6	111	2.7	104	1.3	66
Do	12,511	4.8	192	4.6	147	4.5	180	2.1	112
Do	18,946	3.5	92	3.5	74	2.5	71	1.1	48
Leaves horizontal	21,729	2.6	60	5.2	96	3.5	80	1	31
Do	26,028	5.4	104	7.5	115	4.7	90	1.7	44
Do	19,261	5.7	149	5.5	114	4.5	117	1.2	42
Leaves inclined	25,796	7.3	142	9.2	143	7.2	140	2.9	75
Do	53,335	7.9	74	11.5	80	6.0	56	2.5	31
Do	18,856	5.7	151	8.2	171	4.2	111	2.2	78
Averages:									
Level turf			133		145		180		56
Level gravel			137		130		118		75
Leaves horizontal			104		108		96		39
Leaves inclined			116		131		102		61

Station.	Average hourly standard evaporation.			
	9 to 11 a. m.	11 a. m. to 1h30m p. m.	1h30m to 3h30m p. m.	3h30m to 4h30m p. m.
	c. c.	*c. c.*	*c. c.*	*c. c.*
Level gravel	1.137	2.520	3.800	3.50
Level turf	1.820	2.240	2.970	1.575
Sloping gravel	2.307	3.266	4.260	1.657

Station.	Temperature (° C.).			
	11h20m a. m.	12h45m p. m.	2h15m p. m.	3h30m p. m.
Level gravel:				
3 in. above surface (shade)	19	22.6	21.0	18.0
Soil surface	32	38.0	31.8	25.8
Level turf:				
3 in. above surface (shade)	18.6	21.2	20.6	16.0
Soil surface	18.8	22.2	22.6	20.0
Gravel slope:				
3 in. above surface (shade)	.....	.....	29.8	18.2
Soil surface	.....	.....	45.8	38.0

TABLE 24.—*Short-period phytometers, variability, and sun and shade, September 21, 1923.*

Station.	Leaf product.	9^h40^m to 11^h40^m a. m.		Station.	11^h40^m a. m. to 2^h40^m a. m.		Percentage of sun.
		Loss.	Hourly loss per leaf product.		Loss.	Hourly loss per leaf product.	
		gm.			*gm.*		
Sun	14,110	3.8	135				
Do	20,692	7.5	181	Sun	10.0	121	
Do	12,511	4.8	112	Do	5.6	149	
Do	18,946	3.6	95	Do	3.4	89	
Do	19,261	6.9	178	Half-shade	2.3	40	
Do	25,796	8.5	165	Do	5.1	66	
Do	21,448	4.6	107	Do	2.2	34	
Do	21,729	4.6	106	Do	3.3	51	
Do	26,028	5.1	98	Shade	1.2	15	
Do	53,335	8.6	81	Do	1.7	11	
Do	11,814	5	212	Do	.4	11	
Do	12,969	4.1	157	Do	.3	7	
Average, sun			135.5	Average:			
				Sun		119.6	100
				Half-shade		47.7	39
				Shade		11.0	9

Station.	Average hourly standard evaporation.		Air-temperature, in shade 3 in. above soil surface (° C.).	
	9^h40^m to 11 a. m.	11^h40^m a. m. to 2^h40^m p. m.	12^h50^m p. m.	3 p. m.
	c. c.	*c. c.*		
Sun	2.64	2.83	20.8	[1] 17
Half-shade		1.56	18.2	17
Shade		.84	12	13.8

[1] 21.8° in sun.

TABLE 25.—*Short-period phytometers, slope-exposure, September 26–27, 1923.*

Station.	Leaf product.	8^h30^m to 11^h30^m a. m.		11^h45^m a. m. to 3 p. m.		3 to 6 p. m.		6 p. m. to 6^h45^m a. m.	
		Loss.	Hourly loss per leaf product.	Loss.	Hourly loss per leaf product.	Loss.	Hourly loss per leaf product.	Loss.	Hourly loss per leaf product.
		gm.		*gm.*		*gm.*		*gm.*	
South	34,688	10.8	104	8.1	72	1.7	16	0.8	2
Do	23,747	8	112	5.3	66	1	14	1.1	3
Do	36,627	13.1	119	10.1	85	1.9	17	.5	1
North	35,175	12.2	116	15.5	136	3.8	36	3.5	7
Do	27,616	9.7	105	10.1	113	3.6	43	2.3	6
Do	44,779	12.2	90	[1]9.8	76	4.8	40	1.8	3
Average:									
South	.....	.....	112	.....	108	.....	40	.....	5
North	.....	.....	104	.....	74	.....	16	.....	2
Average standard hourly evaporation:			*c. c.*		*c. c.*		*c. c.*		*c. c.*
South	.....	.....	2.75	.....	3.64	.....	3.25	.....	2.05
North	.....	.....	1.60	.....	3.01	.....	2.52	.....	1.32

Stations.	Temperature, ° C.					
	8^h40^m a. m.	10^h30^m a. m.	12 m.	3 p. m.	6 p. m.	6^h30^m a. m.
South	20.4	22.2	25.1	21.8	13.6	6.4
North	11.4	18.6	19.8	21.3	13.4	6.2

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A. Mixed prairie at plains station, 6,100 feet, Colorado Springs.
B. Montane forest (*Pseudotsuga mucronata*) at montane station, 8,600 feet, Alpine Laboratory.

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A. Subalpine forest (*Picea engelmanni*) at subalpine station, 10,800 feet, Pike's Peak.
B. Battery of large wheat phytometers, montane station, 1920.

A. Battery of sunflower phytometers, plains station, 1918.
B. Battery of sunflower phytometers, montane station, 1918.
C. Battery of oat and wheat phytometers, montane station, 1918.

A. Sun station, 1923. B. Half-shade station, 1923.

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A. Full-shade station, 1923.
B. Photosynthesis and respiration phytometers, sun station, 1923.

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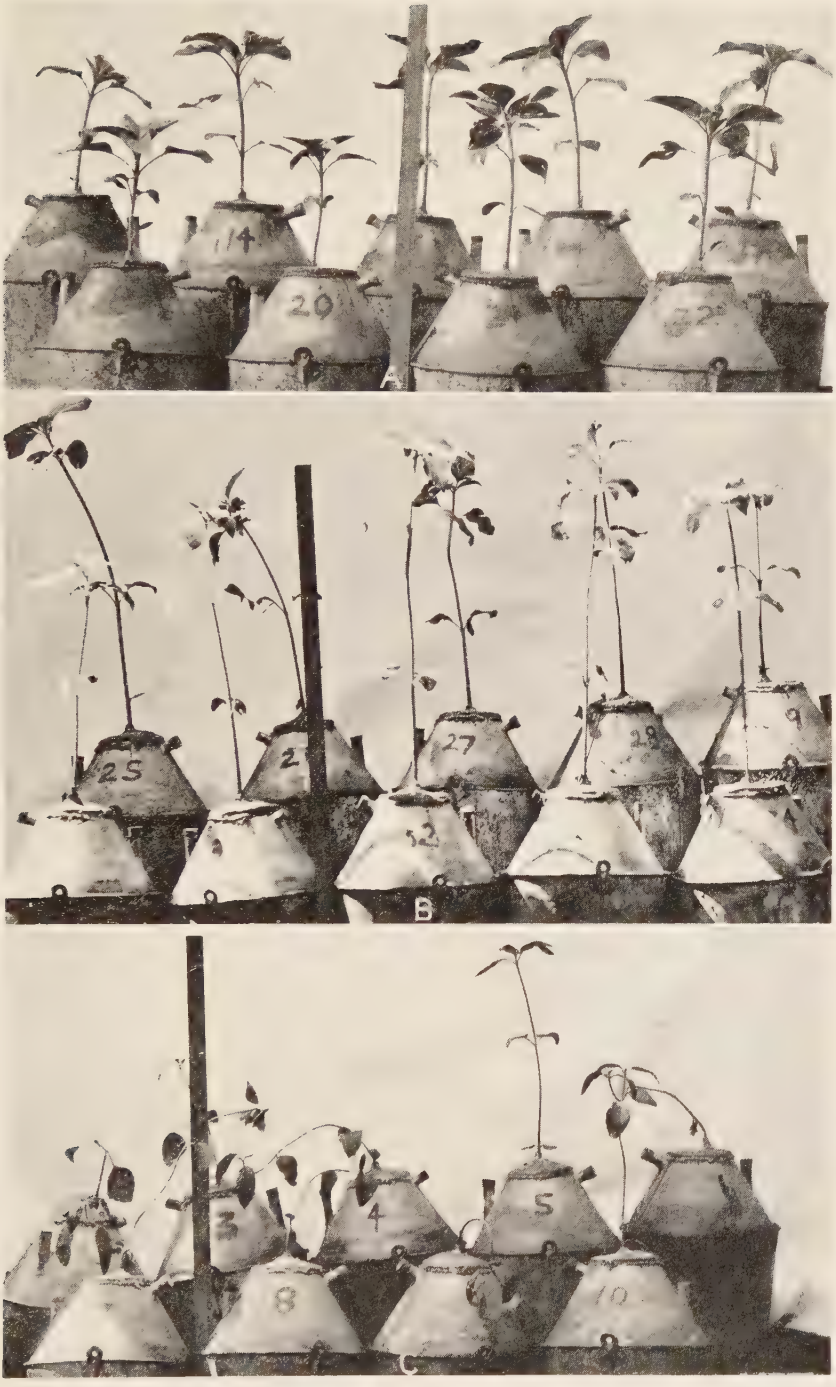

A. Sunflower phytometers, sun station, first series, 1923.
B. Same, half-shade station.
C. Same, full-shade station.

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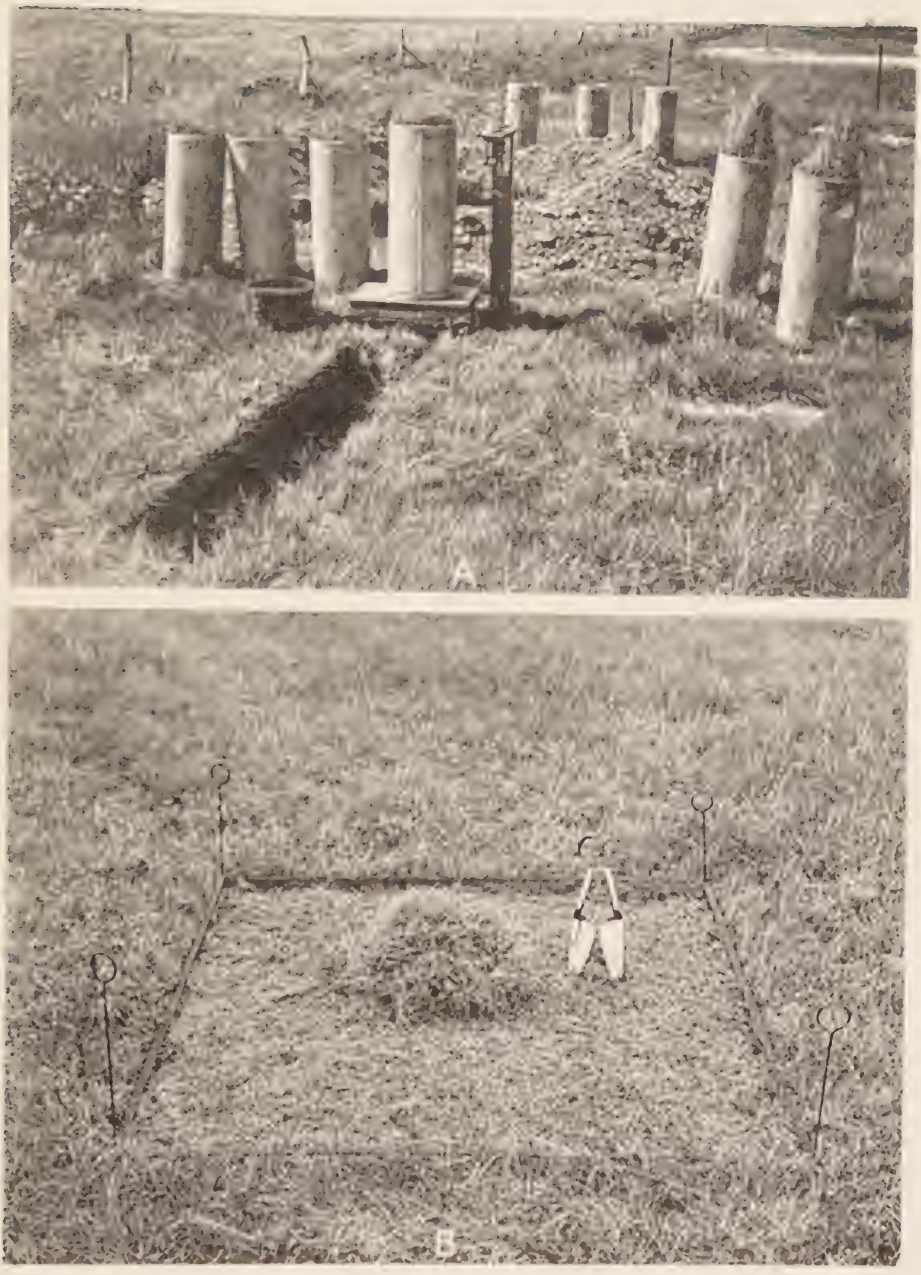
A. Growth of shoots, shade, half-shade, and sun stations, second series, 1923.
B. Growth of roots, sun, half-shade, and shade stations.

A. Battery of sunflower phytometers, slope-exposure transect, mesocline station.
B. Same, canyon-bottom station.
C. Same, xerocline station.



A. Sod-core phytometers and details of installation, Burlington, Colorado.
B. Clip-quadrat phytometer in *Bulbilis-Boutelona* short-grass, Burlington.

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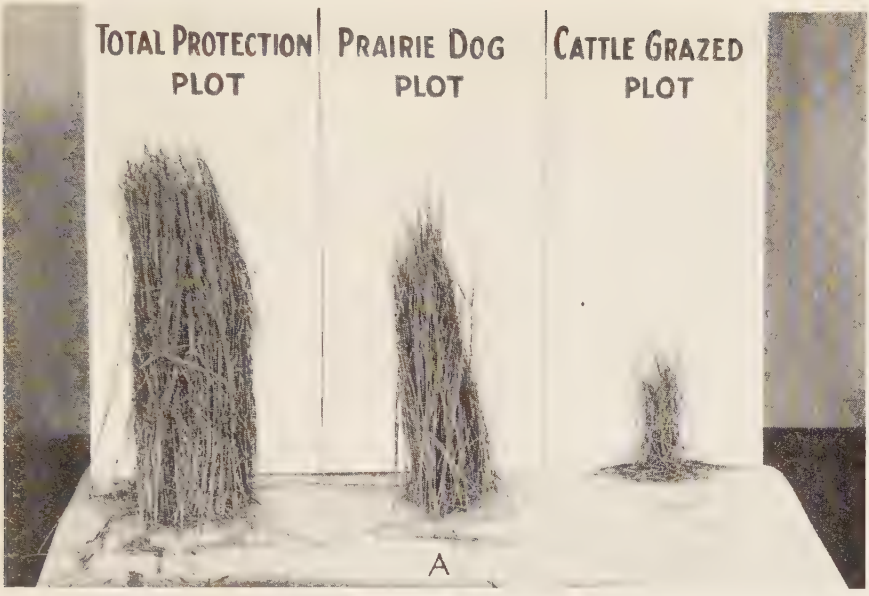

A. *Agropyrum glaucum* from clip-quadrats in cattle-prairiedog inclosure, cattle exclosure, and open range, Grand Canyon, Arizona.

B. Cattle-rodent exclosure. Santa Rita Range Reserve. Tucson, Arizcna, showing growth of desert-plains grassland under complete protection.

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